CILIA;

BY

W. SHARPEY, M.D. F.R.S.E.

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C I L I A.

CILIA,* (in anatomy, Fr. *Cils;* Germ. *Wimperhaare.)* This term is used to designate a peculiar sort of moving organs, resembling small hairs, which are visible with the microscope in many animals. These organs are found on parts of the body which are habitually in contact with water or other more or less fluid matters, and produce motion in these fluids, impelling them along the surface of the parts. The currents or other motions thus produced serve various purposes in the economy of the animals in which they occur. In other circumstances the cilia serve as organs of locomotion, some aquatic animals propelling themselves through the water by their means.

Cilia have now been ascertained to exist in a great many invertebrated and in all vertebrated animals, except Fishes; having been very recently discovered by Purkinje and Valentin on the respiratory and uterine mucous membranes of Mammalia, Birds, and Reptiles.†

The terms " vibratory motion" and " ciliary motion" have been employed to express the appearance produced by the moving cilia; the latter is here preferred, but it is used to express the whole phenomenon as well as the mere motion of the cilia.

A considerable space has been allotted to the present article, more perhaps than its relative importance may seem to demand, chiefly for the reason that, with one exception, no attempt has been hitherto made to collect and describe under appropriate heads, the facts known on the subject. The exception alluded to is a work by Purkinje and Valentin,‡ which appeared while this article was in progress, and which contains not only an account of their own discovery, but a history of all preceding observations. But the manner of treating the subject in the work alluded to is for the most part so different from that which is here followed, that its publication has not seemed to warrant any material abridgement of the following article, which, on the contrary, it has increased by affording much new and important matter, as will be acknowledged in its proper place. Another ground on which indulgence may be claimed for details which are, perhaps, greater than may seem commensurate with the importance of the subject, is that many of the facts are here described for the first time, and it was felt desirable to state them in their full extent, which could not be done intelligibly without considerable length of description.

The article is divided into two parts; the first comprehends the particular facts, or an account of the phenomena as they occur in the different tribes of animals considered in Zoological order, with the history of their discovery; the second part consists of general deductions from the first, and also treats of the structure and mode of action of the cilia in general. This method has been adopted as appearing on the whole best suited to the present state of knowledge on the subject.

PART I.

1. *Infusoria.*— Cilia exist very extensively in the different tribes of Infusory Animalcules; indeed they constitute the principal organs of motion in these small animals. When a drop of water containing Infusoria is brought under the microscope, these creatures are seen swimming rapidly through it in various directions; and as they move along, small particles of foreign matter which happen to lie near their path are thrown into agitation, obviously indicating the existence of currents in the neighbouring water. When the animals remain steady in one place, these currents become much more distinct, setting in particular directions, and causing the small particles to run in a stream to and from the animal. If the magnifying power be sufficiently strong, small transparent filaments will be distinguished, projecting from the surface of the animalcules and moving in a very rapid manner. These are the cilia; they serve like fins or paddles to carry on the animal in its progression through the water, and when it is stationary, they impel the water in a current along the surface, which

* For another signification of this term, see the articles EYE and LACHRYMAL APPARATUS.

† Fishes are no longer an exception; see note at page 29.

‡ De phenomeno motus vibratorii, &c. 4to. Wratisl. 1835.

is beset with them. They may be often most distinctly seen when their motion beeomes languid or impeded, as is the case when the water round the animal is diminished by evaporation to such a degree as not to afford scope for their full and rapid play.

The cilia of the Infusoria in their arrangement are either separate and independent, or combined, forming in the latter case the rotatory or wheel-like organs of the rotiferous tribes of animalcules.

In the first or simple form, which exists in the Polygastric Infusoria (*fig.* 1), the cilia are usually set round the mouth or spread over the body generally, in which case they are often disposed in regular rows. Their strueture has been carefully investigated by Professor Ehrenberg, who states that each is furnished with a bulb at the root, to which minute muscles are attached. A slight degree of rotation communicated to the bulb causes a much more extensive motion in the rest of the organ, which in its revolution describes a eone. From time to time the animal sets its cilia in motion, and then, if its body be free, the cilia, acting like fins or oars, move it onwards through the water, serving in this case as organs of locomotion. If the body is fixed, the cilia communicate an impulse to the surrounding water and excite a current in it. This may always be made evident by mixing with the water some colouring matter, the particles of which are hurried along by the current. Many of these particles are conveyed towards the mouth, where some are swallowed and the rest thrown back, the cilia in this case serving the animal as a means of seizing its food.

Fig. 1.

Leucophrys patula.

In their combined form the cilia constitute the singular and well-known rotatory or wheel-like organs of the Rotiferous Infusoria. These are formed of one or more circles of cilia, placed on the fore part of the animal, as in Philodina (*fig.* 2), in which the organ is double, consisting of two cireles of cilia set on two short processes, one on each side of the mouth. This apparatus ean be retracted or pushed out at the will of the animal. When in motion, the eircles of cilia have the appearance of toothed wheels turned round on their axes, first in one direction and then in the opposite. Various explanations of this apparent revolution have been given. According to Ehrenberg it is an optical deception, which he thus explains: the individual cilia composing the rotatory organ move in the same manner as the separate cilia above mentioned, that is, they each revolve in such a way as to eircumscribe a eonical space. When viewed sideways, in performing this revolution they must necessarily pass at one moment a little nearer, at another a little more distant from the eye, or, in other words, become alternately more and less distinct to the view at short intervals; and this alternation occurring over the whole circle gives rise to a seeming ehange of place in every part of it, and a consequent appearance of rotation. Perhaps it would be an equally satisfaetory and a more simple explanation to consider the appearance as occasioned by an undulatory motion of the cilia, such as that produced by the wind in a field of eorn; the undulations following one another in every part of the circle would give the appearance of rotation. Such a waving motion of the cilia undoubtedly occurs in other animals. The Rotifera set in motion or retract their ciliary organs apparently by a voluntary act; they use them for similar purposes as other Infusoria use their simple eilia; when the body is free, the rotatory organ propels it through the water; at other times the animal fixes itself by its tail, and setting in motion its wheels, produces currents in the water, by means of whieh it seizes its food. These eurrents in most of the Rotifera have a determinate and regular direction.

Fig. 2.

Philodina erythropthalma.

The cilia of the Infusoria, then, serve as organs of locomotion; and in the greater number of species they are the only visible organs for this purpose; indeed it is not improbable that they may exist in others in which from their smallness they have hitherto eluded observation; as in such cases currents are observed which are most probably produced by invisible cilia. Secondly, the cilia are employed by the animals in catching their food. Thirdly, it is extremely probable that, by bringing sueeessive portions of water into contact with the surface of the animal, they serve also for respiration.

Soon after the invention of the microscope, the animalcula of infusions became a favourite subject for its employment, and the cilia and the motions which they produced did not escape the notice of the earlier microscopic observers. Leeuwenhoek observed them distinctly and recognised their use, and probably he was the first that did so. He repeatedly makes mention of them in his writings. At one place* he describes them in an animalcule, which seems to have been the *volvox*, as short slender organs projecting a little from the body, by means of which the animal produced a revolving motion and moved onwards. Again,† in speaking of the animalcules which he obtained from an infusion of pepper, he states that these animals produced a great commotion in the water by means of divers organs placed on the fore part of the head, which organs also the animals used in swimming. " In this way," says he, " they occasioned such a circular eddy in the water that not only several

* Continuatio Arcanorum Naturæ, 1719, p. 382, Epist. 144.

† Continuatio Epistolarum, 1715, p. 95, Epist. 17, Oct. 1687.

small bodies floating in the water were moved in a circular manner, but even many very minute animalcules, though able to swim vigorously, when they approached the larger animalcules, were whirled about for some time in a circular manner." In announcing his discovery of the wheel animal,* he describes its rotatory apparatus as two projecting discs set round with very slender elongated organs. "Imagine," says he, "two wheels set round with points of needles, and moved very swiftly round from west by the south to the east." He adds that he cannot comprehend how such motion takes place in a living body. Lastly, in describing a small animal which he found adhering to the water-lentil, (probably a species of vorticella,) and speaking of the currents which it excites, and by which it attracts its food, he adds the following reflection:† "Moreover it is necessary that these animals, and in general all such as are fixed and cannot change their place, should be provided with an apparatus for stirring up motion in the water, by which motion they obtain any matters that float in the water, for their nourishment and growth and for covering their bodies."

Baker,‡ next to Leeuwenhoek, takes notice of the cilia of animalcules. He observed them in many species, and named them fins, or feet, and sometimes fibrillæ. He distinctly recognised the currents produced by them, and inferred the existence of cilia as the cause of visible currents in cases where the cilia themselves could not be seen.§ In particular, he bestowed much pains in investigating the economy of the wheel animal previously discovered by Leeuwenhoek, and addressed a letter to the Royal Society on the subject, in 1744.‖ He there describes its rotatory apparatus as "a couple of semicircular instruments round the edges of which many little fibrillæ move themselves very briskly, sometimes with a kind of rotation, and sometimes in a trembling or vibrating manner,"¶——"by this means a current of water is brought from a great distance to the very mouth of the creature, which thereby is supplied with many little animalcules and various particles of matter."** He also states that the wheels are instruments of locomotion by which the creature swims.†† Baker drew a distinction between the rotatory and vibratory motions of the cilia, these organs being moved in some animals in the one way, in some in the other, while in others they seemed capable of being used in both ways.‡‡ It appears that he was aware of the true structure of the so-called wheels, and though he often speaks of their being turned round, he was still doubtful of the reality of the apparent rotation.

Spallanzani, in his curious and interesting researches on the production and economy of the Infusoria, made observations similar to those of Baker on the cilia and their motions. He describes them as small filaments or points agitated with a vibratory or oscillating motion. He conceived them to be organs of locomotion which the animals used in swimming,* and that they also served to excite a vortex or current by means of which food was brought to the mouth. "The oscillating filaments cause the vortex; the vortex draws the floating particles into the aperture or mouth of the animalcule, and the latter chooses for its aliment the most delicate, or at least those which suit it best."† He afterwards describes the ciliary apparatus of the vorticella in a similar manner.‡ In the account of his singular experiments on the apparent resuscitation of the *Rotifer*, he describes its wheel organs as two circles of filaments, exactly like the vibrating filaments of other Infusoria, which by their continued motion give rise to the appearance of two moving wheels; but he distinctly states that the rotation is only apparent, not real. These organs, he adds, serve the same purposes as the simple cilia.§

Needham,‖ about the same time as Spallanzani, correctly observed the cilia, and recognized their uses. Saussure¶ observed the currents, but did not perceive the cilia. Pallas,** in his systematic work on Zoophytes, describes the eddies or currents produced by certain Rotifera, and notices their cilia, but far less clearly than his predecessors. Wrisberg†† observed the currents and eddies produced by the vorticellæ; at least he saw smaller Infusoria and particles of floating matter hurried on towards their mouths, but he seems not to have perceived the cilia.

Otto Frederick Müller,‡‡ in his systematic work on the Infusoria, described the appearance and arrangement of the cilia in each species, and represented them in figures. He named them *cilia* and *pili*, and ascribed to their action the currents and vortices which the Infusoria excite. But while he assigns to them the office of locomotive organs, he denies that they are employed in seizing food; for, what is singular, in his long-continued and elaborate inquiries into the economy of these animals, he could never perceive that foreign matters drawn into the mouth were retained there as nourishment, but believed that they were always again thrown out. In this, however, he was undoubtedly mistaken.

* Continuatio Arcanorum Naturæ, 1719, p. 386, Epist. 144.

† Epistolæ Physiologicæ, 1719, p. 66. Epist. 7.

‡ I cite his work entitled "Of Microscopes, and the Discoveries made thereby," London, 1785, although his observations were previously related in separate memoirs of a much earlier date.

§ Of Microscopes, vol. i. p. 71, p. 80.

‖ Reprinted in op. cit. ii. p. 267.

¶ P. 271.

** P. 273.

†† P. 284.

‡‡ P. 292.

* Opuscules de Physique, tom. i. p. 180.

† P. 183.

‡ P. 199.

§ Tom. ii. p. 227.

‖ Spallanzani, Nouvelles Recherches sur les Decouvertes Microscopiques, &c. 1769, p. 161.

¶ See Letter by Bonnet, in Spallanzani Opuscules, tom. i. p. 176.

** Elenchus Zoophytorum, 1766.

†† Observationum de Animalculis Infusoriis satura, 1765, p. 52, p. 63.

‡‡ Vermium Terrestrium et Fluviatilium Historia, 1773, and Animalcula Infusoria, 1788.

Gleichen,* in 1778, described the currents produced by the vorticellæ. In an earlier work he ascribed an agitation of small bodies, which he had observed in the neighbourhood of one of the Infusoria, to an electric or magnetic force, not having perceived the cilia.†

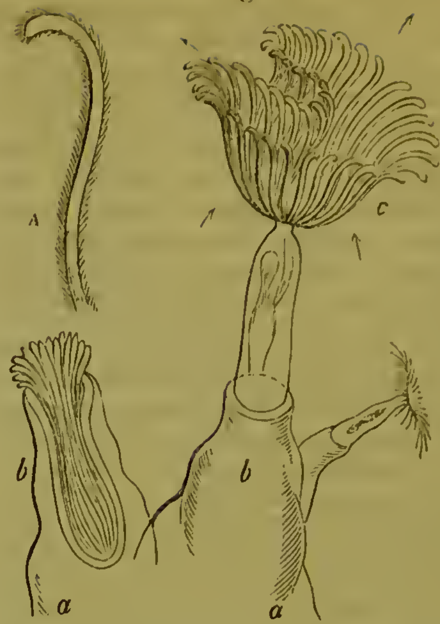
Fontana‡ described the rotatory apparatus of the Rotifer and its use; he conceived that its apparent rotation was produced by the successive elevation and depression of the cilia which encircle it.

Of the more recent writers who have investigated or described these phenomena in the Infusoria, I may mention Dutrochet,§ Gruithuisen,|| Agardh,¶ Raspail,** and Ehrenberg.†† Raspail denies the existence of cilia, attributing their appearance to an optical deception, an opinion which is undoubtedly erroneous. Ehrenberg, who, of all recent observers, has contributed most to the knowledge of the economy and natural history of the Infusoria, has particularly investigated the structure and mode of action of their cilia. The substance of his observations has been already given.

The ciliary motion has been recently observed in the embryo of Infusoria while enclosed in the ovum.‡‡

2. *Polypi and Sponges.—a. Fresh-water polypi.* The phenomena in question have not been discovered in the Hydra, which is the largest and best known of the Fresh-water Polypi; but they have been seen and described by many observers in another sort, viz. that known by the names of the *Polype à panache*, or Plumed Polype of Trembley, the Bell-flower animal of Baker, and Plumatella, Cristatella, Alcyonella, &c. of other naturalists. The Polypes of this kind are connected in groups on a common stock or stem, (*a*, *a*, *fig.* 3, which represents the animal magnified,) and each is furnished with a tube (*b*, *b'*), into which it can wholly withdraw itself. From time to time they advance a little way out of the tubes and display a double row of arms or tentacula (*c*) ranged round the mouth in the figure of a horse-shoe. When the arms are spread out in this manner, currents appear in the surrounding water, which are made evident by the motion of any small particles that may accidentally or intentionally be suspended in it. The currents pass along the tentacula, the water being drawn towards

Fig. 3.



them from every side, and the main stream at last issues from the midst of them, appearing as if it came out of the mouth, from which, however, it really is not derived. The arms are fringed on their two borders with a multitude of cilia, (see A, a single arm magnified,) set close together, which vibrate in regular succession, their motion appearing like progressive undulations along the tentacula. When one of the arms is cut off, it affects the water in the same way as when connected with the animal, its cilia impelling the fluid in a current, or carrying the separated arm through it, according as it is fixed or free.)

As to the use of these motions, it may be stated that they serve undoubtedly for renewing the water in respiration, and probably also to convey food to the animal. Steinbuch, however, remarked that the currents were most lively in pure water, and that the extraneous matters which they conveyed seemed rather to incommode the animal, which endeavoured to avoid them; and from this he inferred that the currents served chiefly if not solely for respiration.

Trembley* and Baker† observed the currents produced by this polype, but both erroneously conceived them to be caused by agitation of the tentacula. Roesel ‡ correctly remarked that, during the production of the currents, the tentacula were motionless, but not perceiving the cilia, nor being aware that the arms when detached still produced motion in the water, he supposed that the currents were occasioned by a stream issuing from the mouth. At length Steinbuch§ discovered that separated tentacula retained the power of impelling the water; he distinguished the cilia and their motion as the cause of the impulsion, and

* Abhandlung ueber die Saamen und Infusions Thierchen, 1778.
† See Müller, Infus. p. 87.
‡ Traité sur le venin de la Vipère, etc. 1781, tom. i. p. 87.
§ Sur les Rotifères, Ann. du Museum d'Hist. Nat. 1812, tom. xix. et 1813, tom. xx.
|| Salzburg. Med. Chir. Zeitung, 1818, iv. p. 222.
¶ Ueber die Zauberkraft der Infusorien, Nov. Act. Acad. Cæs. Leop. tom. x. p. 127.
** Hist. Nat. de l' Alcyonella Fluviatile, etc. Mém. de la Soc. d'Hist. Nat. tom. iv. and Chimie Organique, 1833.
†† Abhandl. d. Akad. der Wiss. zu Berlin für 1831.
‡‡ Wagner, Isis, 1832, p. 383.

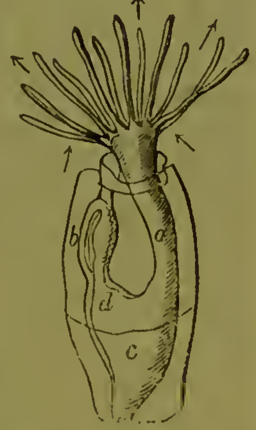
* Mém. pour servir à l'Hist. d'un genre de Polype d'eau douce, 1744, p. 212.
† Of Microscopes, ii. p. 309.
‡ Insecten Belustigungen, tom. iii. 1755, p. 458.
§ Analecten neuer Beobachtungen und Untersuchungen für die Naturkunde, 1802, p. 89.

more correctly described the course of the currents: the foregoing description is in a great measure taken from his memoir. Since then several others* have made similar observations, among whom we may mention Raspail as more particularly deserving of notice, though he here, as in other cases, denies the existence of cilia.

b. Marine Polypi.—The polypi of marine Zoophytes, on which observations relating to the present subject have been made, may for our purpose be conveniently arranged under three principal forms.

The first form of polype (*fig.* 4) is found in Flustræ and cellular polypi generally; it exists also in some species which have been classed among the Sertulariæ, and probably prevails very extensively in different tribes of Zoophytes. The body (*a*, *b*, *c*), which is generally contained in a cell, is bent on itself, somewhat like the letter Y or V; the one branch (*a*) being the mouth and throat, the other (*b*) the rectum opening by an anus, and the middle part (*c*), which is of a dark and often of a brown colour, being the stomach probably with some accessory organ. The mouth is surrounded with a variable number of long straight tentacula or arms, fringed on both of their lateral margins with cilia. When the arms are expanded, the cilia are thrown into rapid motion, which has the appearance of undulations proceeding along the fringes, upwards on one side of the arm or from its root to the point, and downwards on the other. While the cilia are thus moved, they produce currents in the water, as described in the Fresh-water Polype, and here also the currents in all probability serve for respiration and the prehension of food. Besides these motions in the water in the neighbourhood of the tentacula, a revolving motion of particles is observed within the body: small particles of extraneous matter which enter the throat are moved round within it; and the contents of the stomach and rectum undergo a very singular revolving motion round the axis of the cavity. These internal motions, Dr. Grant conjectured, might be owing to internal cilia; and I have been able to satisfy myself of the actual existence of such internal cilia, by means of a Wollaston's doublet of one-thirtyfifth of an inch focus; they are very evident in the throat; in the stomach they are most distinct in the part adjoining the rectum (indicated by *d* in the figure), and they are clearly to be seen on the whole internal surface of the rectum (*b*).

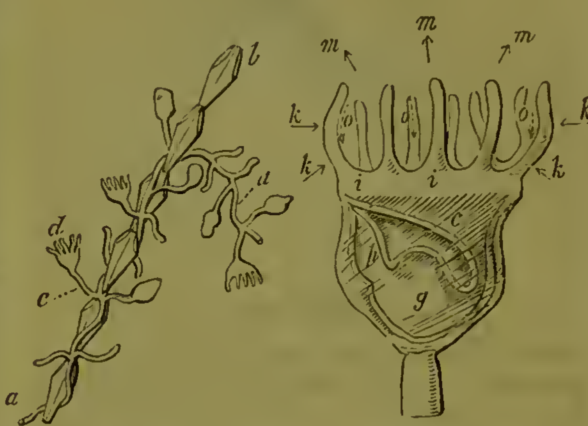
Fig. 4.



Polype of a Flustra in its cell.

I have nowhere more clearly seen the above-mentioned phenomena than in a zoophyte, whose polype, though differing somewhat from the first form, may yet be referred to it. This zoophyte (*fig.* 5, A, B) has a creeping stem

Fig. 5.



A B

(*a*, *a*), which adheres to shells, or twines round the stems and branches of other zoophytes, (as *b* in the figure); the polypes are supported on soft pliable fleshy stalks (*c*), which the creature moves from time to time; their body (*d*, and B more magnified) is bell-shaped and consists of a transparent brownish skin or envelope containing the mouth and throat (*e*), the stomach (*g*), and rectum (*h*). The mouth, or expanded aperture of the animal, is surrounded by a prominent lip or border (*i*, *i*), to which the arms are attached. Cilia are distinctly visible on the arms, and within the mouth and stomach; they are moved very briskly, and small extraneous particles indicating currents in the water are hurried onwards towards the arms, as pointed out by the arrows at *k*, *k*; many of these particles descend along the inner side of the arms to their base, as shown by the dotted arrows *o*, *o*, *o*, and thence into the cavity of the mouth, from which, after being moved about for some time, the greater number are thrown out. It would seem that the particles of food or other solid matter, after being conveyed to the inside of the arms, take then a different course from the stream of water. The latter passes inwards between the arms, and issues from the middle of the irregular circle which they form (as at *m*, *m*), carrying with it such solid matters as are not arrested on the arms; but the bodies which enter the mouth are slowly carried along the inside of the arms (as at *o*, *o*), and in close contact with them till they reach their base. The motions of the contents of the stomach and its cilia appeared as in the Flustræ. I could perceive none in the rectum. Mr. Lister has described the same phenomena in a zoophyte closely resembling this one in the structure of the polypi, but differing in the character of the stem.*

* Vaucher, Bull. de la Soc. Philom. An xii.; Raspail, Mém. de la Soc. d'Hist. Nat. de Paris, for 1827; Meyen über Polypen, Isis 1828, p. 1225.

* Phil. Trans. for 1834, p. 385.

In the second form (*fig.* 6) the stem and branches are formed externally of a tough (generally horny) substance, and within this of a transparent soft tissue, which is tubular and contains a granular matter. The polypi resemble hydræ; each is lodged in a horny cell (*a*, *a*), from which it partially protrudes itself; one orifice surrounded with tentacula serves both for receiving aliment and discharging fæces; this leads to a stomach (*b*), which communicates through an opening (*c*) at the bottom of the cell with the interior of the tubular stem and branches, the attached part or base of the polype being continuous with the soft internal tube, of which the polypes might be regarded as a prolongation. In this form of polype, which exists in most true species of Sertularia, Campanularia, and Plumularia, and in allied genera, the tentacula or arms are destitute of cilia and incapable of giving an impulsion to the water. But a very remarkable motion has been observed by Cavolini* and Mr. Lister,† in the granular matter contained in the stem and branches. Although this motion has not been traced to the agency of cilia, yet as it is connected with our subject, I shall briefly notice it here. When the stem and branches of the above-named zoophytes are examined with a high magnifying power, a current of granular particles is seen running along the axis of the tube. The current, which is compared to the running of sand in a sand-glass, after continuing one or two minutes in the same direction, changes and sets in the opposite one, in which it continues about as long, and again resumes the first, thus alternately flowing along the stem to the extremities of the branches, and back again. The change of direction is sometimes immediate, but at other times the particles are quiet for a while, or exhibit a confused whirling motion for a few seconds before the change takes place. Mr. Lister has discovered that the currents extend into the stomachs of the polypi, in which and in the

Fig. 6.

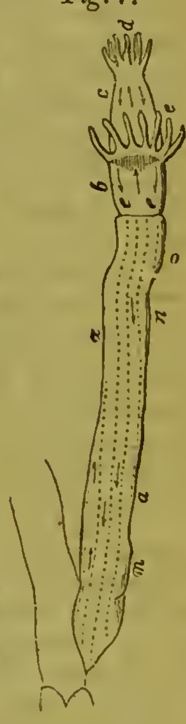
Campanularia.

* Memorie per servire alla storia de' Polypi Marini, p. 121 and 197; p. 56 and 91 of the German Translation.
† Phil. trans. 1834, p. 369.

mouth a remarkable agitation of particles is perceptible. When these particles are allowed to escape from a cut branch, they exhibit, according to Mr. Lister, something very like spontaneous motion. The immediate cause of these currents is not apparent; it seems not to be muscular contraction of the tube; perhaps, like the agitation within the stomach, they may be owing to internal cilia. As to their use Mr. Lister supposes the circulating matter "to be a great agent in absorption, and to perform a prominent part in the obscure processes of growth; and its flow into the stomach of the polypi seems to indicate that in this very simple family (the Sertulariæ) it acts also as a solvent of the food."—Page 77. Perhaps the polypi of the Pennatula and Virgularia should be referred to this head. In these Dr. Grant* discovered a constant vibratory motion within the mouth, apparently produced by cilia placed round the entrance of that passage, and he saw minute particles occasionally propelled from the mouth. Their tentacula, as in the zoophytes last referred to, did not excite currents.

The third form of polype is found in Tubularia. *Fig.* 7 represents a magnified view of a common species, the Tubularia indivisa. There is a transparent horny tube (*a*, *a*), containing a soft matter, which at the extremity of the tube is continuous with the stomach (*b*) and the mouth (*c*). There are two rows of tentacula or arms, one (*d*) immediately surrounding the orifice of the mouth, the other (*e*) further back, between the mouth and stomach. The arms are destitute of cilia and excite no movement in the water; but Mr. Lister† has discovered a remarkable motion of particles within the tube, which has some resemblance to the circulation of globules observed in plants of the genus *Chara*. These particles moved in a current within the tube, the general course of the stream being parallel to the slightly spiral lines of spots on the tube, and in the directions marked by the arrows. On the greater part of the side first viewed (the one represented) it set as from the polypus; but on the other side the flow was towards the polypus, each current thus occupying half the circumference. The tube had a granulated appearance between the lines of spots, and beneath this the particles ran. Their course was even and uniform without any starting or dancing motion, such as is observed in the Sertulariæ. At the nodous parts of the

Fig. 7.



Tubularia indivisa.

* Edin. Phil. Journ.
† Phil. Trans. 1834, p. 366.

tube (m, n) were slight vortices in the current, and at o near the end of the tube it came over from the opposite side. Two currents were continually going on in the mouth and the stomach, one always flowing down the sides in the direction e, e, and the opposite one in the axis. Neither the cause of these currents nor their use has been ascertained.

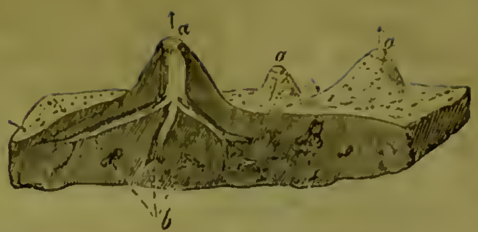
Such are the phenomena of the ciliary and other apparently allied motions in the Marine Polypi.

Spallanzani seems to have first noticed them; he observed the currents produced by the Flustræ, but erroneously attributed them to the agitation of the arms, the cilia on which he had not perceived. Dr. Fleming* described the current along the tentacula in the Valkeria cuscuta (a genus which he has separated from the Sertulariæ, among which it was previously included,) and distinguished the cilia with their undulatory motion. Dr. Grant† discovered the cilia on the arms of the Flustræ and described their undulatory motion, to which he ascribed the motion in the water. He also pointed out the revolving motion of particles within the mouth, stomach, and rectum, and conjectured that it was owing to the action of internal cilia, which conjecture I have been able to verify. Dr. Grant also discovered the vibratory and probably ciliary motion within the mouth of the polype of the Pennatulæ. Loefling‡ first observed the agitation of granular matter within the stem and branches of the Sertulariæ. Cavolini afterwards more correctly described this as a current of fluid holding granules in suspension, running first in one direction and then in the other. Lastly, Mr. Lister observed anew these internal currents of the Sertulariæ, described them more minutely, and showed that they extended into the stomach of the polypes. Mr. Lister has also described the phenomena in the Flustræ previously observed by Dr. Grant. He discovered the currents within the stem of the Tubularia, which, as far as I know, had not been previously noticed.

c. *Sponges.*—In the various species of sponges, water, the element in which they live and grow, passes in currents through pores and canals in their substance, in a continuous manner, entering at one place and issuing at another. This phenomenon has not been directly traced to the agency of cilia; it comes nevertheless to be considered here, as such an agency is highly probable, and at least the motion of the water is not owing to any contraction of the canals in which it flows, but is obviously caused by some other kind of impulsion communicated to it by the surface along which it passes.

In a common sponge we see a number of pretty large orifices on the surface, each opening on the summit of a conical eminence or papilla (*fig.* 8, *a*). These openings are named

Fig. 8.



Sponge.

by Dr. Grant the "fæcal orifices." Innumerable small *pores* occupy the rest of the surface, and give to it its peculiar character. These pores penetrate to a certain depth, and lead into canals (b), which, uniting together and gradually growing larger, terminate in wide tubes, which open at the fæcal orifices. The pores, excretory canals, and fæcal orifices thus form continuous passages through the sponge. In the fresh state they are lined throughout with a smooth gelatinous coating.

When a living sponge is examined attentively in its native element, the water is perceived entering at the pores and issuing from the fæcal orifices, its course being indicated by the motion of any floating particles that may be present. The issuing currents are stronger than the entering, and are rendered conspicuous by excrementitious matters or sometimes ova, conveyed out at the fæcal orifices.

When sections of the sponge, including a greater or less extent of the internal canals, are placed in water, the fluid, according to Dr. Grant's observations, is still evidently moved along the internal surface of the portions of canals, although their continuity with the rest is destroyed. Dr. Grant could not detect cilia either in these canals or the pores which lead to them, but he discovered these organs on the ova of the sponge, which thereby execute remarkable spontaneous motions, and he is inclined to attribute the currents in the adult sponge also to cilia, which he conceives may probably exist, though, from their smallness, he has not been able to perceive them. At any rate he has shewn by most satisfactory observations, that the current cannot be ascribed to contractions in the canal, for in none of his numerous experiments instituted for the purpose, could he discover any sign of irritability, at least any sign of contraction of the tissue of the sponge on the application of stimuli.

Naturalists even of the earliest times, whose attention was directed to the phenomena exhibited by the living sponge, have remarked that water entered and passed out from its porous substance, but the true course of the fluid seems to have been unknown, it having been erroneously supposed to enter and issue by the same orifices. Dr. Grant,* to whose labours we owe most of the correct information obtained respecting the structure and functions of the sponge, demonstrated that the current is continuous, and flows always in one direction as above described, and proved that the motion

* Mem. of Wern. Soc. fol. p. v. p. 488.

† On the Structure and Nature of Flustræ. Ed. New Phil. Journal, vol. iii. 1827.

‡ Schwedische Abhandlungen, 1752, p. 121.

* Edin. Phil. Journal, vols. xiii. xiv. Edin. New Phil. Journal, vols. i. and ii.

of the water was not produced by contraction and dilatation of the tissue of the sponge, which he showed to be destitute of irritability. Dutrochet had made observations on the same subject, which were published subsequently* to those of Dr. Grant, and not anteriorly as he supposes; he perceived the constant direction of the current, and ascribed the phenomenon to *endosmosis* and *exosmosis*.

3. *Ciliary motion of the ova of Polypi and Sponges.*—The ova or gemmules of several of these zoophytes execute independent movements, and produce currents in the surrounding water. This singular fact was, it appears, first noticed by Mr. Ellis in 1755,† in examining a species of Sertularia, the Campanularia dichotoma; but he described the ova or embryos which he had seen in motion, as young polypi, already somewhat advanced in their formation. Cavolini,‡ in 1784 and 1785, observed the same phenomenon in the ova of the Gorgonia and Madrepore, and investigated it more fully. He saw the egg-shaped gemmules or ova, on quitting the parent, rise to the surface, and swim with their large end forwards, in a horizontal direction, till they fixed themselves on some spot where they were developed. Dr. Grant,§ in 1825, discovered similar motions in the ova of the sponge, and detected the moving cilia. The cilia covered the whole surface of the ovum, except the posterior tapering extremity, and in its motions the large end of the ovum was always directed forwards. When an ovum fixed itself, its cilia still continued to play, by which a current along its surface was kept up for some time. Dr. Grant also investigated the movements of the ova of the Campanularia, previously seen by Ellis, and of the Plumularia falcata. The ova of both these zoophytes are contained within transparent capsules, two or more being in each capsule, surrounded by a clear fluid. Dr. Grant distinctly perceived cilia vibrating on the surface of the ova, and causing, while within the capsule, an eddying motion of the surrounding fluid, but propelling the ova through the water when extracted from their capsule, as in the sponge. The ciliary motion has also been found in the ova of fresh-water polypi, having been discovered by Meyen‖ in those of the Alcyonella stagnorum, which is probably the same with, or at least nearly allied to the bell-flower polype.

By means of the remarkable provision here described, the ova of these fixed zoophytes are disseminated, and conveyed to situations suitable to become the abode of the future individuals. The same provision undoubtedly serves also to move the water along their surface for the purpose of respiration. It exists, as will be afterwards shown, in the ova of many other animals.

* L'agent immediat du mouvement vital devoilé, 1826, p. 179, and Annales des Sciences Naturelles, 1828, tom. xv. p. 205.

† Hist. Nat. des Corallines, p. 116.

‡ Memorie per servire alla storia de' Polypi Marini, Nap. 1785, p. 8, p. 48, of German translation.

§ Edin. New Phil. Journal, vol. i. p. 150.

‖ Isis, 1828, p. 1225, sqq. Isis, 1830, p. 186.

4. *Acalephæ.*—Many species of Medusæ are furnished with cilia, or at least with moving organs bearing a close resemblance to the cilia of other animals, though in the Medusæ they present several peculiarities. The cilia are found in all the Medusæ belonging to the order *Ciliograda* of Blainville, or *Ctenophora* of Eschscholz, of which the genus Beroe is a good example. Eschscholz* describes them as small pectinated or comb-like organs, ranged in longitudinal rows or stripes on the external surface of the body, with their flat surfaces in apposition. Each comb-like organ consists of many small, flattened, pointed filaments, united together by a common base, the points being directed towards the posterior extremity of the body. They are moved like fins, being slowly raised and suddenly struck back, by which means the body is carried through the water. In the Beroë and others of similar form, the cilia point towards the closed extremity of the body, so that the opposite or open end is carried forward. The animal seems to have the power of moving more or fewer of these organs as it may incline, by which means other motions besides direct progression are performed. The cilia, when separated from the body with a piece of skin, continue to move briskly for some time. A longitudinal vessel runs under each row of cilia, communicating with the rest of the vascular system, and containing a fluid, in which yellowish particles are suspended. Eschscholz regards these vessels as arteries, and considers the cilia as respiratory as well as locomotive organs. Dr. Grant, in describing the cilia of the Beroë pileus,† represents the parallel filaments of which the comb-like organs consist, as united together by a membrane as far as their points, like the rays in the fin of a fish.

Schweigger compares the vessels which run underneath the rows of cilia, to the canals communicating with the tubular feet of the Sea-urchin and Asterias; and Dr. Grant seems also inclined to ascribe the motion of the cilia, whose filaments he conceives to be tubular, to their being alternately filled and emptied of fluid derived from the longitudinal vessel, like the tubular feet of the Echinodermata. This view of their mode of action, however, is scarcely reconcilable with the observed phenomena, as will be afterwards shown in considering the structure of the cilia in general. Audouin believed that in the Idya, a genus nearly allied to the Beroë, the fluid of the longitudinal vessel, which he supposes to be water, is sent into the cilia; he therefore regarded them as respiratory organs. If the vessel under the cilia in this case, as in the Beroë, communicate with the rest of the vascular system, and its contained fluid be regarded as blood, then the cilia of the Idya, which, according to Audouin, are permeated by the fluid, would bear a certain analogy to the gills of fishes.

* System der Acalephen, p. 3.

† Zoological Trans. vol. i. p. 9.

Cilia appear also to exist in other tribes of Medusæ besides the Ciliograda, but they differ in form and situation from those described, and have not been investigated with equal accuracy.

In Rhizostoma there are certain membranous appendages attached to the arms or tentacula, and bearing on their free edge a fringe of short filaments which are constantly in motion, and continue so for some time after the arm or portion of membrane supporting them is detached from the body. These filaments are described and figured by Eysenhardt,* who regards them as organs of generation; they are probably of the nature of cilia. Similar filamentary organs seem also to exist within the body in some Medusæ. (See ACALEPHÆ, p. 48.)

5. *Actiniæ.*—In a paper published on the present subject in 1830,† I mentioned that I had found the ciliary motion in the Actinia or Sea-anemony, but gave no description of it. I have since re-examined various species of Actiniæ with this view, and shall now describe the appearances; but to make the description intelligible, it may not be improper to remind the reader of some points in the anatomy of these animals which require to be kept in view.

The body of the Actinia, of which *fig.* 9.

Fig. 9.

Actinia.

is a plan, consists entirely of a soft but tough substance, exceedingly contractile and irritable. It is usually cylindrical in shape, one end, (*a*, *a*,) named the base or foot, serving to fix the animal by adhering to rocks or other objects; the other extremity is named the disc, one-half of which is seen at *b*, *b*, the other half being removed by a section; it is surrounded at its circumference by the arms or tentacula (*c*, *c*,) in concentric rows, and in its centre is the mouth (*d*), or opening of the stomach, which serves both for the entrance of food and discharge of undigested remains. The stomach (*e*) is plaited longitudinally on its inside; vertical membranous partitions (*g*, *g*, *g'*, *g'*,) pass from its outer surface to the inside of the parietes of the body, and to the base, dividing the intermediate space into numerous compartments or cells, which communicate with each other by openings, as at *g'*, *g'*, and also open into the tentacula, as at *h*. The latter are conical muscular tubes, communicating at their base with the cells, and opening at their point by a small orifice, surrounded by a sphincter muscle. The cells seem also to communicate with the cavity of the stomach, and, according to Rapp,* they open in some species by small orifices on the surface of the body. The cells and tentacula contain sea-water, with which the animal can distend the whole body or any particular part of it. The protrusion of the tentacula, as is well known, is effected by their distension with water. The stomach also is often partially everted and protruded from the mouth by an accumulation of water behind it. It has not, so far as I know, been clearly shewn by which of the communicating orifices the water enters. Though I took considerable pains, I have not been able satisfactorily to ascertain this point; I may remark, however, that I have repeatedly noticed water entering at the mouth.

The ovaries and oviducts (*k*, *k*,) are lodged in the cells, and are consequently bathed in water; of these it is unnecessary here to say more than that one part of them consists of a waving membranous fold like a mesentery, attached by one edge to the sides of the cell, and at its free border supporting the oviduct, which resembles a white opaque chord, terminating, after numerous serpentine windings, in the stomach.

In regard to the ciliary motion in the Actiniæ, I am led from my observations to conclude that it exists to a greater extent in some species than in others. In all cases I have found it on the surface of the oviducts and their supporting membranes, which is covered with cilia of very minute size; also on the internal surface of the stomach, which has similar cilia, and there the currents follow the direction of the folds of the membrane. In one small but full-grown species I found currents commencing near the centre of the disc, and proceeding outwards in a radiating manner to its circumference, whence they continued along the arms as far as the points. On examining this species, which was semitransparent, by transmitted light, I distinctly perceived moving particles in the water contained within the tentacula and behind the protruded stomach.† The motion of these particles obviously indicated a current in the water along the surfaces containing it, which current, like that on the oviducts, it may be inferred was produced by cilia, for it went on while there was no perceptible contraction taking place in any part of the animal. The particles indicating the currents

* Nova Acta Acad. Cæs. Leop. vol. x. p. 404.
† Edin. Med. and Surg. Journal, vol. xxxiv.

* Ueber die Polypen und die Actinien. Weimar, 1829, p. 47.
† Some of these particles were no doubt the ova.

within the tentacula, were moved in two different directions, namely, from the base to the point, and from the point to the base; and (supposing the arm spread out horizontally,) the outward current was along the under part of the tube, and the returning one along the upper: (see *h*.) I also observed these internal currents of the tentacula in a young specimen of Actinia senilis, which seemed to have been very recently discharged from the parent; in it also there were radiating currents on the disc, but they stopped at the base of the tentacula. Thus the external currents on the disc and tentacula were found in one species, and they occur on the disc in some other species in the young state, but their occurrence in this situation is by no means general in adult Actiniæ.

The phenomena described are in all probability connected with the processes of nutrition and respiration. They bear a striking analogy to those I have observed in the Echinodermata.

The ova of the Actiniæ were observed by Rathke to revolve round their axis, and occasionally to move straightforwards in the water. He could detect no cilia or other moving organs.*

6. *Echinodermata.*—The animals of this class in which I have observed the ciliary motion, are different species of the Sea-star *(Asterias)*, and the Sea-urchin *(Echinus)*. In proceeding to describe the phenomena in the Asterias, I must first take the liberty of explaining some points in the anatomy of that animal, referring the reader for other details to the proper sources, especially the monograph of Tiedemann.†

On the under surface of the Asterias, (I speak of the Asterias rubens in particular, *fig.* 10, A, B, C, as it is a large species and common on our shores,) we observe the mouth in the centre, and the tubular feet *(l, fig.* B) projecting in rows along the under part of the rays. Nearly the whole surface of the animal is beset with three kinds of eminences. First, hard calcareous processes, *(a, fig.* C,) placed like studs at some distance from each other. Secondly, claw-like processes (*b*, *b*); these singular organs are more thickly set; they consist of a solid stem of soft substance, bearing at the extremity a sort of pincers or forceps of hard calcareous matter, like the claw of a crab. They resemble analogous organs found on the Sea-urchin, only that the maxillæ or pincers in the latter consist of three pieces; they were named antennæ or feelers by Monro, but Müller regarded them as parasitical animals. The third sort of processes (*c*, *c*,) are named the respiratory tubes, and are the most important in regard to our present subject. They are short, conical, membranous tubes, communicating at their base with the internal cavity of the body, and perforated at their point by an orifice which can be very perfectly closed. Most of them are placed in groups or patches, and, corresponding with each group of tubes, the fibrous membrane forming the wall of the body presents on its inside a pit or shallow depression (*e*), perforated with holes, through which the tubes communicate with the general cavity. Like the tentacula of the Actiniæ, which they resemble in several other respects, they can be distended with water and elongated, or emptied, contracted, and shortened.

Fig. 10.

A, *Asterias viewed from above.* B, *Cross section of a Ray.* C, *Part of the section at m, fig.* A, *magnified.*

* Dorpater Jahrbüch. für Litt. Stat. und Kunst. Bd. i. Heft. i. p. 84—86, quoted by Purkinje and Valentin, p. 32. I have since seen the independent motion of the ova when extracted from the animal. It was shown to me by Mr. Graham Dalyell, who had long before observed it. The cilia could be distinctly perceived.

† Anatomie der Röhren Holothurie, &c. Landshut, 1816.

In the inside of the body the membranous stomach *(g)* occupies the middle part, and from it a pair of lobed cœca *(h, h,)* (and *i, i,* cut short) pass into each ray. Within the rays also we find inferiorly the rows of vesicles *(k, k)* which form part of the feet *(l, l)*, and the ovaries. All the rays communicate through the middle part, and the whole inside is lined by a transparent membrane *(n, n)*, which, like a sort of peritoneum, covers the stomach and cœca, attaches each of the cœca by a mesentery *(o, o)* to the roof of the ray, lines the fibrous parietes of the body, and is probably reflected over the vesicles of the feet and the ovaries. Each mesentery encloses a space *(o, fig.* B) between its sides, which opens into the general cavity at the root of the cœca. The lining membrane passes into the perforated pits *(e)*, by which the tubes *(c)* communicate with the cavity, and sends prolongations through the perforations into the tubes lining them to their points. The space *(s, s, fig.* B) lined by this membrane contains sea-water, which is generally described as entering and issuing by the respiratory tubes.*

I find the ciliary motion in four situations, namely, 1. on the external surface; 2. within the cavity of the body, or in the space *(s)* between its parietes and the viscera; 3. within the stomach and cœca; 4. within the feet. In all these situations moving cilia are visible with the microscope on the respective surfaces; they are every where comparatively small, in some parts excessively so. Though I have not traced them over the entire extent of each surface, I have no doubt they exist at every point where currents are produced.

1. On the external surface. The ciliary motion as indicated by the application of powdered charcoal, occurs over nearly its entire extent, but with different degrees of intensity. The strongest currents pass along the outer surface of the tubes from the base to the point, as at *c′*; they are also pretty strong on the claw-like processes *(b′)* and intermediate skin; on the feet they are evident but less vigorous.

2. Within the body the currents take place on the lining membrane and its reflections. A longitudinal current runs along the roof, and another along the floor of each ray, forwards or towards its point: (see the arrows in *fig.* A.) These advancing currents are confined to the median line and its immediate vicinity; two retiring currents *(r, r,)* run backwards (one on each side) at the place where the sides join the floor of the ray. Two longitudinal currents also exist on each of the cœca, an advancing one *(h′)* on the inferior surface, and a retiring one superiorly (*h, h, fig.* A) in the space *(o, fig.* B) inclosed within the mesentery, which, as already mentioned, opens into the general cavity. The longitudinal currents, except those within the mesentery, are, if for the sake of explanation we may so express it, connected by others which run vertically and transversely on the cœca and on the roof and sides of the cavity, (see the arrows in *fig.* B;) on the vesicles of the feet the course of these cross currents is varied by the curved surfaces. As the lining membrane of the cavity extends into the respiratory tubes, so currents exist within these likewise, as at *t*, *fig.* C. This is proved by injecting turbid fluid into the ray, when particles are seen moving within the tubes; and if a few of the tubes with a portion of the skin be cut off and placed under the microscope, the fluid which will still be retained by some of them may be seen to be in motion, the floating particles moving from the base to the point and back again, as in the arms of the Actiniæ.

3. The motion is very distinct on the inner surface of the stomach and cœca; the currents within the cœca follow the same direction as on their external surface, that is, an advancing current runs inferiorly from the root to the point and a returning one superiorly; and at the sides currents run upwards, following the ridges or folds of the internal membrane which result from the lobulated structure of the cœca.

4. The ciliary motion exists distinctly within the feet, though the cilia are very small; these became visible on viewing the edge of a folded portion with Wollaston's doublet of one-thirty-fifth of an inch focus.

The currents described, as far as I have been able to perceive, preserve always the same determinate direction. Even when portions of the ciliated surface are detached, the motion on them continues, and its direction is the same as before their separation.

As to the use of these motions, it is most probably connected chiefly with respiration; and if such be the case, it would show that in this animal a great extent and variety of parts are concerned in that function. The ciliary motion on the inner surface of the stomach and cœca is probably subservient also to the process of digestion. It is conceivable that by means of this provision the dissolved or digested food might be introduced into the cœca, and spread over their internal surface, there to be duly mixed with secreted fluids, and subjected to the process of absorption; the returning current serving to bring back the residue, or to convey secreted fluids into the stomach. Or, considered as subservient to respiration, the ciliary motion, in diffusing the digested food over the internal surface of the cœca, may at the same time expose it to the respiratory influence of the water on their outside.

These phenomena in the Asterias seem not to have been previously noticed. Tiedemann,* it is true, had observed an eddying motion of the water in the vicinity of the respiratory tubes while the animal was slowly distending or emptying itself, but he conceived it to be nothing more than the commotion necessarily produced by the passage of the water through the tubes. There can be little doubt that the

* Without denying this mode of entrance, I may yet mention, that though I have often seen the animal slowly distending itself with water, and again partially emptying itself, I could never perceive the fluid entering or issuing at the orifices described.

* Anat. der Röhren Holothurie, etc. p. 40.

phenomenon he saw was caused by the ciliary motion on the external surface, though he was not aware of this.

Having entered into these details respecting the Asterias, I may describe more briefly the phenomena in the Sea-urchin, the more so as my opportunities of observing this animal have been less frequent.

The species submitted to examination was the common large Sea-urchin of our shores, Echinus esculentus, described by Monro.* Its body consists of a globular shell, containing the viscera. The mouth is placed underneath, the anus opposite on the upper surface. The tubular feet are disposed in vertical rows from the mouth to the anus, the intermediate part of the shell being covered with moveable spines, and the singular claw-like organs referred to in describing the Asterias. As in the Asterias, there are membranous respiratory tubes, but they are comparatively few in number, forming ten small bunches or groups, which are placed on the under surface not far from the mouth, and open internally in ten small perforated pits, like those of the Asterias; they are supposed by Tiedemann and others to be the channels by which the sea-water gets into the interior of the body, and fills the space between the inside of the shell and the contained viscera. The alimentary canal, commencing at the mouth, rises through the curious dental apparatus named Aristotle's lantern, turns in a waving manner twice round the inside of the shell, and terminates above at the anus; it is supported by a mesentery derived from a membrane which lines the cavity of the shell, and which is reflected over its contents like a peritoneum. Inside the shell we also find the ovaries and the rows of feet. The internal parts of the latter, instead of being round vesicles as in the Asterias, are broad laminæ enclosing vessels,† canals or branched cavities, which canals, like the vesicles of the Asterias, communicate on the one hand with the tubes of the feet, and on the other with a common vessel which runs along the middle of each double row of laminæ. The vessels or spaces within the laminæ are much branched; they form a plexus surrounded by a principal vessel at the border.

I have found the ciliary motion over nearly the whole surface of the cavity of the body and the contained parts, which surface, as mentioned already, is covered by a lining membrane or peritoneum. Two longitudinal currents run on the intestine in the same direction, viz. one along the line of attachment of the mesentery, the other at the opposite part of the tube. On the remaining circumference of the intestine the impulsion is directed obliquely towards the nearest longitudinal current. In regard to the laminæ of the feet, a current runs down the middle of each of the double rows, following the course of the longitudinal vessel there situated, the direction being from the anus towards the mouth. Lateral currents pass over the surface of the laminæ from their external to their internal border, where they join the middle current; they follow the irregular elevations on the surface of the laminæ occasioned by the canals or vessels in the latter; hence, when charcoal powder is applied, the particles follow winding paths in crossing from one edge of the laminæ to the other, and they are frequently caught in a hollow between two currents, and whirled about for some time before they resume their way. Currents were visible also on the reflections of the lining membranes which cover and pass between different parts of the lantern, and at the internal openings of the respiratory tubes. The cilia on the parts described are excessively small, but distinctly perceptible. The ciliary motion was not detected on the external surface of the body nor within the alimentary canal; but in regard to these parts the observations could scarcely be considered as conclusive; nor could I determine whether, as in the Asterias, the phenomenon occurs within the feet or within the spaces or vessels of their membranous laminæ, though from an observation of Carus, who states that he saw globules circulating within these laminæ, its existence in that situation is not improbable.*

This provision in the Echinus is probably, as in the analogous cases already described, chiefly subservient to respiration. Tiedemann, who ascribed a respiratory office to the water within the animal, expresses himself at a loss to conceive by what mechanism it can be made to enter and issue from a cavity with unyielding sides incapable of being expanded and contracted by muscular action; perhaps the provision here described may be adequate for this purpose. Since the above observations were made, a fact has been mentioned by Ehrenberg,† from which it appears that the ciliary motion exists on the external surface of the Echinus on the spines. The species observed by him was the Echinus sexatilis. The observations of Carus and Ehrenberg here referred to comprehend the only facts hitherto published on the ciliary motions of the Echinus which have come under my notice.

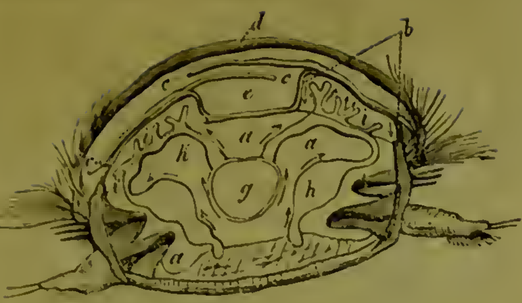
7. *Annelida.*—In proceeding to describe the ciliary motion in animals of this class, in several of which it occurs, it seems advisable to begin with the Aphrodita, as the phenomena in this animal present a remarkable analogy with those we have been considering in the Echinodermata.

A great part of the body of the *Aphrodita aculeata*, or Sea-mouse, (of which *fig.* 11, A, represents a cross section,) is occupied by the abdominal cavity, *(a, a, a.)* Along the superior wall of this cavity a row of cells *(b)* is placed on each side, which below open into the abdomen, but above, or exteriorly, project on the dorsal surface as oblong transverse eminences. Each alternate cell on the back bears a broad membranous scale *(c, c)*, and each of the intermediate ones a small indented process. On the back a covering of felt-like substance *(d)* is stretched from side to side like a roof over

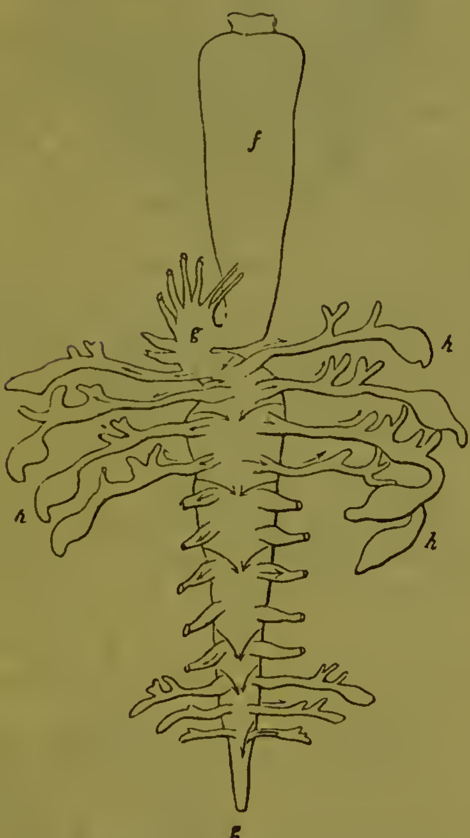
* Anatomy of Fishes, &c.
† Accurately described by Monro, l. c.

* Analecten zur Natur-wissenschaft, etc. Dresden, 1829, p. 152.
† Müller's Archiv. Band 1, p. 578.

Fig. 11.



A. *Cross section of the Aphrodita aculeata.*



B. *Alimentary canal and cœca, seen from above.*

the cells and scales, inclosing them in a space *(e)* to which the water has free access. Returning to the abdomen, we find the nearly straight alimentary canal, its anterior third *(f, fig.* B) forming the stomach, the remaining part or intestine *(g, fig.* A and B) being furnished on each side with a number of long cœca *(h)*, whose branched extremities *(i, i)* are in part lodged in the before-mentioned cells. The abdomen is lined with a delicate peritoneal membrane, which also lines the cells, and is reflected over the viscera.

In the living Aphrodita the water freely enters and issues from the space (*e*) beneath the felty membrane, passing over the external surface of the cells and their appendages. The flow of the water in this passage is produced, as I have repeatedly observed, by the elevation and depression of the scales, and on no part of the surface over which the fluid passes is the ciliary motion to be observed. But the water also enters the cavity of the abdomen, though it is doubtful by what orifices this takes place, for my endeavours to find those described by Treviranus* in the alternate intervals of the feet have never been successful. In whatever way it may happen, however, there can be no doubt of the fact that the water enters the abdomen, and consequently fills the dorsal cells and surrounds the intestine and its cœca, which last organs, according to Sir Everard Home and Treviranus, exercise a respiratory function, an opinion which derives additional probability in considering the phenomena of the ciliary motion to be here described. The ciliary motion exists in two situations, 1st, on the external surface of the intestine and cœca and the internal surface of the cells, which surfaces are in contact with the contained water; 2dly, within the intestine and cœca, or on their internal surface. The motion as usual persists for some time in detached parts, and the direction of the currents is constant. On the intestine the currents pass from the inferior surface round the sides to the upper part (as marked by the arrows). On the cœca the direction is outwards or towards the cells, and the motion is very distinct at their extremities. The direction on the inner surface of the cells was not completely made out, but it seemed to be chiefly downwards. Nor was the direction of the impulsion satisfactorily ascertained on the internal surface of the intestine and cœca, though of the existence of the phenomenon in that situation there could be no doubt.

From what has been stated, it appears then, first, that in the Aphrodita the water finds access to the outside of the cells, over which it is conveyed by the elevation and depression of the dorsal scales, and to the inside of the cells, over which, as well as over the external surface of the intestine and its cœcal appendages, it is moved by the action of cilia. In both situations the motion of the fluid is probably subservient to the respiratory function, and if it really be so, we must reckon the scales, the cells, the alimentary canal, and its appendages, as constituting the respiratory apparatus. Secondly, that the ciliary motion exists also on the internal surface of the intestine and cœca, where it is likely connected both with respiration and digestion. In all this we cannot overlook the analogy which subsists between the Aphrodita and Asterias. In both the water is conveyed, though by a different mechanism, over the external surface of the body; in both it enters the cavity containing the viscera; in both it is moved along the parietes of the cavity and surface of the viscera in a determinate direction by the agency of cilia; and, lastly, in both the ciliary motion occurs on the internal surface of the digestive organs.

I first observed the ciliary motions in the Aphrodita aculeata in 1830, at the same time with the late Mr. Cheek, who gave notice of the fact in the journal of which he was conductor;† but most of the observations on

* Zeitschrift für Physiologie, Band iii. p. 158.
† Edin. Jour. of Nat. and Geog. Science, April, 1831, p. 246.

which the preceding account is founded, were made more recently. There is no mention of the existence of the phenomenon in the Aphrodita to be found in systematic works on comparative anatomy, nor in any of the special memoirs on that animal which I have had an opportunity of consulting.

The ciliary motion exists in several other animals belonging to the class Annelida. It is remarkably distinct, and easily observed, on the branchiæ or gills of the Serpula. These organs consist of two bunches of pinnated or feather-like processes, which the animal pushes forth from the calcareous tube in which it lives, and spreads out in a radiating form. The edges of the branchiæ, both of the stems and of the leaflets, are fringed with cilia, which exhibit their vibrating and undulating motions, and cause a constant current of water over the surface of the gills, serving here, no doubt, as in analogous instances, at least chiefly for respiration.

In a paper already referred to,* I mentioned having observed the phenomena in question in the Amphitrite. The animal meant was a common marine tubicolar worm (*fig.* 12), which

Fig. 12.

Amphitrite alveolata.

A. Dorsal surface, natural size.
B. Part before *a*, *b*, magnified.
C. A gill magnified.
D. One still more magnified, to show the spiral ridges and cilia.

appeared to be the same with that figured by Ellis (Corall. plate 36), and described by Cuvier as the *Amphitrite à ruche*, with which figure it agrees, except that it bears two rows of simple filaments on the back, which, for reasons that will appear, I was led to regard as gills. But if these are really gills, the animal must, it seems, be arranged with the Dorsibranchiata, probably as a Sabella. The currents in this worm proceed forwards along the back, between the rows of gills (as marked in *fig.* B), and along the gills themselves (see C), whose points are directed forwards. The conical filament of which each gill consists is marked on one side by ridges (see C, D), crossing it obliquely like segments of a spiral; and on these ridges as well as on the point of the gill the most conspicuous cilia are placed. The cilia are comparatively large and curved, their points being turned towards the summit of the gill, which figure they retain when their motion is stopped. The gills contain large

* Edin. Med. and Sur. Jour. vol. xxxiv.

bloodvessels, which when distended give them a bright red colour.

The ciliary motion occurs also on what seem to be the branchiæ of another tubicolar worm, the name of which is unknown to me; the organs in question are placed at the anterior extremity of the animal, concealed by a profusion of long serpentine tentacula.

Lastly, Mr. Cheek* observed the ciliary motion in the Sandworm (*Arenicola piscatorum*). It was seen on the inner surface of the internal vesicles, which Sir Everard Home describes as livers. Nothing similar exists on the tufts of filaments which form the gills.†

8. *Mollusca.*—The ciliary motion prevails very extensively in this division of the animal kingdom. It seems to exist generally in the Gasteropodous and Acephalous Mollusca. There is some uncertainty as to its existence in the Cephalopoda; I have repeatedly sought for it in that class, but without success.

It occurs on the surface of the respiratory organs, and often on other surfaces over which the water has to pass in the act of respiration. It also exists within the alimentary canal, at least this has been ascertained in several species of Gasteropoda and Acephala, and may be presumed of the rest. Moreover, in some of the Gasteropoda, it is very manifest on the horns or feelers, which suggests the possibility of its aiding in these instances in the exercise of the sense of touch or smelling. In all cases the impulsion maintains a determinate direction, which continues the same in parts detached from the animal. In salt-water species, the action of the cilia and impulsion of the fluid, are instantly stopped by putting the parts into fresh water.

The ciliary motion also occurs in the embryo of the Mollusca within the egg, which phenomenon will be considered in the next section.

A. *Gasteropodous Mollusca.*—Of this class the phenomena have been observed by myself and others in the orders of *Nudibranchiata*, *Cyclobranchiata*, *Pectinibranchiata*, and the aquatic *Pulmonifera*, in one or more species of each.

a. Nudibranchiata.—In this order, in which the gills are entirely exposed, the currents can be very easily observed. The Doris, a species of which is represented in the adjoining figure (13), may serve as an example. The arborescent gills (*a*, *a*) are ranged in a circle round the anus, and their stems and branches are covered with cilia. Currents pass over their surface, the general direction being towards the points; small portions detached still excite currents in the same direction, and, if free, move through the water in the opposite one. I have examined three species of Doris, and

* Edin. Journ. of Nat. and Geog. Science, April, 1831. p. 245.

† The ciliary motion has also been observed in Planariæ, on the surface of the body, by Gruithuisen, (Salzb. Med. Chir. Zeit. 1818, vol. iv.) and by Purkinje and Valentin Gruithuisen also discovered it in the Nais proboscidea, in the posterior part of the intestine, (Nov. Act. Acad. Cæs. Leop. xi. p. 238.)

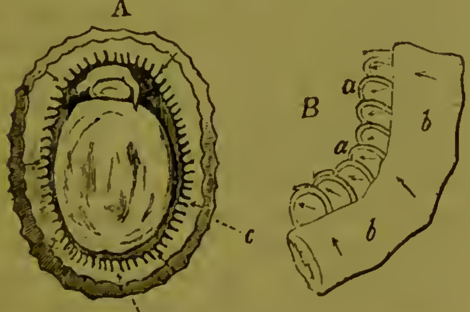
Fig. 13.

Doris.

in one of them, the D. cornuta, the ciliary motion was very strong on the club-shaped feelers; perhaps it may be the same in all. I also examined the Tritonia and Eolis belonging to this order, and found the ciliary motion in corresponding parts.

b. *Cyclobranchiata.*— In the Patella or Limpet (*fig.* 14, representing the under surface), the gills form a series of simple

Fig. 14.



Patella.

B. Portion inclosed between the lines *c* and *d*, magnified to show *a*, *a*, the branchial laminæ, and *b*, *b*, the circular border of the mantle.

laminæ (*a*, *a*) attached within the circular border of the mantle (*b*, *b*). The currents pass inwards from the edge of the mantle to the gills, then over the surface and along the border of each branchial lamina, from its outer or lower to its inner or upper edge, as indicated in the figure by the arrows. In the Limpet the ciliary motion is also found on the inner surface of the alimentary canal.

In the Chiton or Oscabrion (*fig.* 15), the only other genus of this order, the gills are situated as in the Limpet, but are of a more complex structure. Each consists (at least in the species examined by me) of a triangular lamina, with a series of smaller laminæ set on each side of it, diminishing in size as they approach its point. The currents on each of the gills are directed towards its apex, and also pass between the secondary laminæ over their surface and along their edges: *a*, *a*, are the gills; *b* one of the gills magnified, showing its laminæ; *c* the same viewed endwise. The arrows mark the direction of the currents.

Fig. 15.

Chiton.

c. *Pectinibranchiata.*— The common Buccinum (*fig.* 16) may serve as an example of this order. The gills, as accurately described by Cuvier, are attached to the roof of a branchial cavity or recess formed between the mantle (*a*, *a*) and upper part of the body (*b*) in the last turn of the shell, and opening anteriorly by a broad slit. At the left end of the slit the edge of the mantle is prolonged in the form of a groove (*c*), which prolongation is called the syphon, and is lodged in a corresponding groove of the shell. On detaching the roof of the branchial cavity at the left side, and reflecting it (as represented in the figure), we find attached to it, first, the gills, consisting of a short double row (*d*) and a longer single row (*e*) of laminæ, the latter being larger; secondly, to the right of the gills, the so-named mucous laminæ (*f*, *f*); thirdly, still more to the right, the rectum (*g*).

Fig. 16.

Buccinum Undatum.

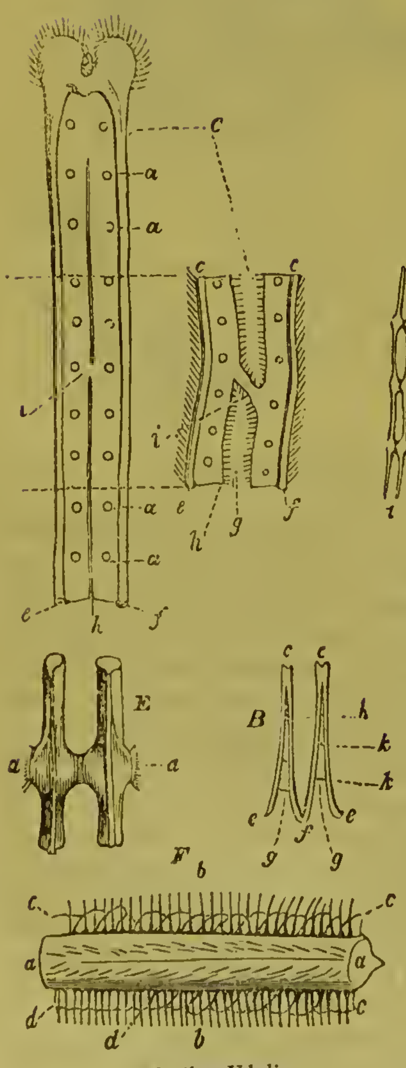
The water enters by the syphon, and issues at the right extremity of the branchial slit. The ciliary motion and currents take place on the gills, mucous laminæ, and rectum, and on

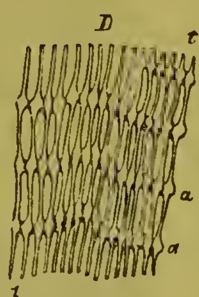
the inner surface of the mantle, where it forms the roof of the branchial cavity. Their situation and direction are indicated in the figures by the arrows. B is an enlarged view of a few laminæ from the larger series, *h* the attached border, *i* point, *m* left, and *n* right border. Currents pass between these laminæ along the surface and border of each, as shewn in B; C is a magnified view of the laminæ of the smaller set, on which the direction of the currents is marked; the direction on other parts will be understood by referring to figure A.

The ciliary motion is very manifest within the alimentary canal, in the gullet, stomach, and intestine; the direction of impulsion is from the mouth towards the anus.

The ciliary motion has been observed by myself and others in the Paludina vivipara, a fresh-water snail belonging to this order,

Fig. 17. A





Mytilus Edulis.

F. Portion of a bar of the gill, with the cilia, highly magnified.

in which also Purkinje and Valentin state that they observed it within the alimentary canal; and Gruithuisen* has described the phenomenon as seen on the branchiæ of another fresh-water snail, which he names Valvata branchiata. He saw moving cilia, which caused an incessant agitation in the water; but he does not state whether the motion followed any constant direction, although we may infer that this was the case. He rightly attributed to these motions a respiratory function, but seems not to have observed that similar phenomena existed in other Mollusca.

d. Pulmonifera. The ciliary motion is not confined to those Mollusca which breathe by gills, for it occurs also in the Lymnæa and Planorbis, which, though they live in water, breathe air by a pulmonary sac. In these instances the impulsion of the water takes place on the surface of the tentacula, which is covered with cilia. If these parts are to be regarded as organs of sensation alone, the ciliary motion observed upon them, as well as that which occurs on the tentacula of branchiferous species, must be considered as connected with the function of sensation; but the tentacula, which in the Lymnæa are broad vascular laminæ, might be conceived also to perform the office of accessory organs of respiration, in which case the pulmoniferous Mollusca here mentioned would possess organs both of aerial and aquatic respiration. In the Lymnæa the motion has also been observed by Purkinje and Valentin within the alimentary canal.

B. *Conchiferous Acephala.*—The motion in question has been found in several bivalve Mollusca, both of salt and fresh water, and there can be little doubt that it exists in all.

The common Sea-mussel (*fig.* 17) will serve as an example of the class. It will be recollected that the gills of this animal (*fig.* A, *c*, *c'*, *d*,) have the form of

* Nova Acta Acad. Cæs. Leop. x. p. 437.

leaves, there being two on each side inclosed between the lobes of the mantle (*a*, *a*, *a'*, *a"*). Between the gills are interposed what is called the foot (*f*) and the prominent part of the abdomen, which separates the two of the right side from those of the left. Each gill or leaf consists of two layers, which are made up of vessels set very close to one another (*fig.* D,) like the teeth of a comb, or like parallel bars, across the direction of the gill, and perpendicular to the great vascular trunks running along its base, with which they communicate. The two layers composing each gill are connected together at its edge, and by a few points of their contiguous surfaces. At the base only one layer is fixed, the other terminating at this part by a thick unattached border (*e*, *e*), under which a probe may be passed into the interior space between the two layers. This is further explained by *fig.* B, which represents a section of the two gills of one side cut parallel to the bars. The layers (*e c*, *f c*,) are united at the edge of the gill (*c*), but separated at the base, the one being fixed at *f*, the other ending by a free margin, *e*. *g*, *g*, is the space between the layers; it communicates with the excretory orifice (*h*, *fig.* A). *Fig.* C shews the upper part of the gill, (*c*, *h*, *fig.* B,) viewed similarly, but magnified eighteen diameters. Two bars, (*e c*, *f c*,) belonging to opposite layers, are seen; they are shaped somewhat like the blade of a knife, with a thick round external border (*e*), and a thin internal edge (*h*) opposed to the corresponding one of the other layer, with which it is connected at a few places by cross slips, *i*, *i*, *fig.* C, and *k*, *k*, *fig.* B, where they are longer, the space at this part being wider. *Fig.* D is a small portion of one of the layers, (*t*, *t*, *fig.* A,) magnified eighteen diameters. The bars are connected laterally with the adjacent ones of the same layer at short intervals, by round projections on their sides, (*a*, *a*, *a*, *a*, *in figs.* D, C, and E,) in which last they are still more magnified. Each of these projections adheres but slightly to the corresponding one of the collateral bar, and its surface is covered with small filaments resembling the cilia in the other parts, only their motion is very slow. Besides the gills, the mussel has four triangular laminæ (*m*, *m*, *n*, *fig.* A,) placed round the mouth, which probably serve for respiration; they have been named labial appendages, tentacula, or accessory gills.

When a live mussel is placed in a vessel of salt water, it is soon observed to open slightly the two valves of its shell, and at the same time a commotion is evident in the water in its vicinity. This is occasioned by the water entering at the posterior or large end of the animal into the space between the lobes of the mantle in which the gills are lodged, and issuing near the same place by a separate orifice in a continued stream, as represented by the arrows, (*g* and *h*, *fig.* A), *g* being the entering and *h* the issuing stream. The existence of this continuous current is well known, but the agency by which the water is set in motion appears not to have been, at least generally, understood. It can readily be shewn that here, as in the instances already described, the water receives its impulse from the ciliated surface of the gills and other parts over which it passes, and that it is carried along these surfaces in a determinate direction. The whole surface of the gills and labial appendages or accessory gills, the inner surface of the cloak, and the surface of some other parts produce this effect, and the combined action of the cilia over this extensive surface gives rise to the main current which enters and issues from the animal.

On removing one of the valves, turning down the cloak, as represented at *o*, and putting moistened charcoal powder on the surface of the gills, the finer part of the powder soon disappears, having penetrated through the interstices of the bars or vessels into the space between the two layers of the gill. On arriving there a part is often forced out again from under the border of the unattached layer at the base of the gill, but most of it is conveyed rapidly backwards between the two layers, and is carried out at the excretory orifice with the general current, its course being indicated by the dotted arrows in the figure. The coarser particles remain outside the gill, and are slowly carried to its edge, following the direction of the bars; they then advance along the edge of the gill towards the forepart of the animal, as shewn by the entire arrows. It thus appears that the water first passes in between the lobes of the mantle to the external surface of the gills; it is then forced into the space inclosed between their layers, from whence it is driven out at the excretory orifice, to which the inclosed spaces of all the gills lead. As this process continues to go on after the shell and lobe of the mantle of one side are removed, it is evident that the motion of the water must be mainly produced by the cilia of the gills, to be immediately described. By their agency the fluid is forced into the space within the gills, and this operation taking place over the whole extent of the gills, must, by its concentrated effect, give rise to a powerful issuing stream at the excretory orifice, of which the entering stream seems to be a necessary result.

The cilia are found on the gills, the accessory gills, the inside of the mantle, and the foot. Only those on the gills require particular notice. Most of them are arranged along the sides of the vessels or bars (*a*, *a*, *fig.* F), composing the gills, in two sets, one nearer the surface consisting of longer and more opaque cilia, (*b*, *b*,) the other close to the first, but a little deeper, and consisting of somewhat shorter and nearly transparent cilia, (*c*, *c*.) Both sets are in constant motion, but of this it is difficult to convey a correct idea by description. The more opaque cilia, or those of the exterior range, appear and disappear by turns, as if they were continually changing from a horizontal to a vertical* direction and back again. The

* By vertical is here meant a direction perpendicular to the plane of the gills, which direction is vertical when the gills are spread out under the microscope.

motion of the other set consists in a succession of undulations, which proceed in a uniform manner along the sides of the bar from one end to the other. It might be very easily mistaken for the circulation of globules of a fluid within a canal, more especially as the course of the undulations is different on the two sides of the bar, being directed on one side towards the edge of the gill, and on the other towards the base. But besides that the undulations continue for some time in small pieces cut off from the gill, which is inconsistent with the progression of fluid in a canal, the cilia are easily distinguished when the undulatory motion becomes languid. When it has entirely ceased, they remain in contact with each other, so as to present the appearance of a membrane, (*d, d, fig.* F.) Besides the two rows of cilia just described on each side of the bars, others are placed in a less regular manner on their external and internal borders. The internal (*h, fig.* C) are exceedingly small; they extend upon the cross slips, (*i, fig.* C). Those on the external borders are very numerous and thick-set, and of considerable size, especially on the extremity of the bar at the edge of the gill (*c, fig.* C); their points are directed towards the edge of the gill. It is probably by the agency of these last-mentioned cilia that the particles of food or other foreign matter are conveyed along the surface of the gill to its edge, and then onwards to the mouth, while the others may serve principally to force the water through the interstices of the bars into the space inclosed between the layers, and from thence out at the excretory orifice.

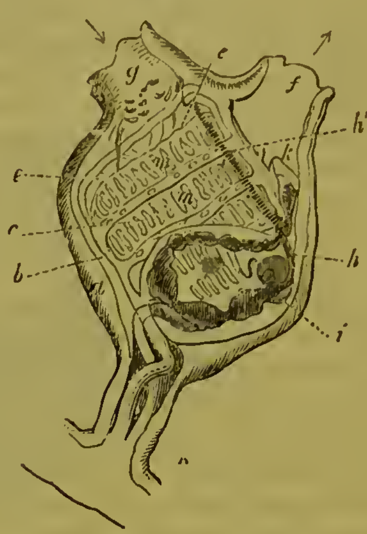
As in other instances, detached portions of the ciliated parts excite currents in the same direction as before their separation, or swim through the water in the opposite direction. It is very remarkable that when the parts are immersed in fresh water, the currents and motion of the cilia are almost instantaneously stopped.

The ciliary motion is equally apparent on the respiratory organs of the Oyster, River-mussel, and other bivalve Mollusca which have been submitted to examination. Purkinje and Valentin pointed out its existence also in the alimentary canal of the River-mussel, which observation I have confirmed, and I have found the same to be true of the Sea-mussel. The impulsion appeared to me in both instances to be chiefly directed onwards, that is, towards the anus.

c. Tunicata (Ascidiæ).—In the paper previously referred to, I stated that I had not been able to perceive the ciliary motion in the Ascidia, but added that the observation seemed inconclusive, as the specimens examined had been some time out of the water. Since then I have seen the phenomena as distinctly in the Ascidiæ as in other Mollusca. The observations were made on a common species found adhering to rocks in the Frith of Forth at low water-mark, and as far as they go they agree with those lately made by Mr. Lister,* on a small aggregated species, the substance of which being nearly transparent enabled him to trace the currents more completely. For this reason it seems preferable to borrow his description.

The annexed figures (A and B) represent

Fig. 18.



one of these Ascidiæ on its peduncle, with the opening of the mouth (*g*) and the funnel (*f'*) in front. The outer covering is a tough coat (*a*), lined internally with a soft substance or mantle (*b*). A great part of the interior is occupied with the branchial sac (*c*), whose cavity terminates upwards at the oral opening, and is closed at the bottom. It is united to the envelope or to the mantle above and behind; the juncture (*e, e,*) beginning in front of the oral opening, extends backwards on each side of it, and then downwards along the middle of the back (*a', fig.* A.) A vacant space (*f, f,*) is left between the sac and mantle at the sides and front, which ends in the opening of the funnel. The sac opens inferiorly into the œsophagus (*h*), which leads to the stomach (*i*), the intestine passing forwards and opening by the vent (*k*) into the funnel. On its sides and front the branchial sac is perforated by four rows of narrow vertical slits or spiracles (*m, m*), and through these the water, which flows constantly in at the mouth when its orifice is open, appears to be conveyed to the vacant space (*f*) between the sac and mantle, and it then escapes at the funnel. The sac seems extremely thin between the spiracles, but their edges are thickened, and they are lined with closely set cilia, which, by their motion, cause the current of water. When they are in full activity, the effect upon the eye is that of delicately toothed oval wheels, revolving continually in a direction ascending on

* Phil. Trans. 1834, p. 378.

the right and descending on the left of each oval, as viewed from without; but the cilia themselves are very much closer than the apparent teeth, and the illusion seems to be caused by a fanning motion given to them in regular and quick succession, which will produce the appearance of waves, and each wave answers here to a tooth.

Whatever little substances alive or inanimate the current of water brings, if not ejected as unsuitable, lodge somewhere on the surface of the branchial sac, along which each particle travels horizontally with a steady slow course to the front of the cavity, where it reaches a downward stream of similar materials *(h')*; and they proceed together, receiving accessions from both sides, and enter at last, at the bottom, the œsophagus *(h)*; this is a small flattened tube which carries them, without any effort of swallowing, towards the stomach.

Mr. Lister observed similar phenomena in a species of Polyclinum, another form of compound Ascidia, in which an excretory funnel is common to several individuals. Mr. Lister, p. 385, has adverted to the resemblance between the Ascidiæ and a zoophyte of a similar form to that here described at page 7. I may here point out an analogy on the other side, no less striking, between the Ascidiæ and bivalve Mollusca, in regard to the phenomena now under consideration. In both cases the water enters at one opening, and meeting with the surface of the membranous gills, passes through slits or interstices between their vessels into a space on the other side of the gill, which space terminates at another external opening, by which the water issues. In both cases also the margins of the slits in the gills are fringed with cilia which exhibit a waving motion, the waves proceeding in opposite directions on the two borders of the slit. Lastly, in both cases, while the water and finer particles of matter floating in it pass through the slits, the coarser matters are conveyed along the first surface of the gills towards the mouth. The difference lies chiefly in the nature and form of the external covering and the form of the gills in each; the membranous gills in the mussel being folded into double leaves on each side, and in the Ascidia being formed into a tubular sac; the space between the laminæ of each leaf in the mussel corresponding with the space *(f)* enclosed between the branchial sac and mantle in the Ascidia, both these spaces leading to the excretory orifice.

The remarkable appearances in the Mollusca described above could not wholly escape the notice of naturalists and microscopic observers. Thus we find Ant. de Heide,* a Dutch physician of the end of the seventeenth century, observing the appearance produced by the ciliary motion in the Sea-mussel; he names it "motus radiosus," or "tremulus." He found it in most parts of the animal, but in none more evident than the gills (cirri pectinati), in which it is most easily examined. "I call the motion radiant," says he, "because it proceeds from the whole surface of the cirrus (gill) almost in the same way as air-bubbles issue from crabstones or metals while undergoing solution; it may be called tremulous, because the parts affected by it vibrate. This motion goes on not only in the entire gill connected with the rest of the mussel, but even in the smallest pieces cut off from it, which by their radiant motion swim briskly through the sea-water."

* Anat. Mytuli, &c. 12mo. Amst. 1684.

Leeuwenhoek likewise appears, from various passages in his writings,* to have perceived the moving cilia in the Oyster and Mussel; he noticed also the existence of the motion in detached portions. His observations, so far as they go, are correct; but he takes no notice of the currents in the water; nor does he seem to have perceived the relation of the phenomenon to the respiratory or other functions, or indeed to have formed any opinion regarding its physiological use.

Baker alludes to Leeuwenhoek's discoveries, and relates an appearance observed by himself in the Fresh-water Mussel, which must have been caused by the ciliary motion.† He states that "on snipping off a piece of the transparent membrane (gill), and viewing it with the microscope, the blood will be seen passing through numbers of veins and arteries, and if the extremity of the membrane be viewed, the true circulation or the return of the blood from the arteries through the veins will be shewn." Dr. Hales, in his Statical Essays, (vol. ii. p. 93,) plainly alludes to the same phenomena. Among more recent writers, Professor Ehrman of Berlin, in a memoir on the blood of the Mollusca, published in the Transactions of the Royal Academy of Sciences of Berlin for 1816-17,‡ has described an appearance noticed by him in Mya, Anodonta, the Oyster, and other Bivalves, which seems evidently to have been produced by the ciliary motion. He states that on viewing the inner side of the labial appendages, accessory gills, or tentacula of these Mollusca, while it was illuminated by a strong light falling in a particular direction, he perceived a very rapid and incessant motion along the transverse stripes or furrows observable on the surface of the part. The motion proceeded along each stripe like a series of oscillations. It continued for some time in portions cut off from the organ. He next observed that a number of round vesicular bodies escaped from the furrows or stripes at the part where they were cut, which bodies moved to and fro and as it were spontaneously in the water; and it seemed to him that in proportion as these bodies escaped, the oscillatory motion relaxed in intensity. From these facts he concluded that the motion apparent on the surface of the part was produced by the agitation of these vesicles or animated molecules within the furrows; that is, he supposed the furrows to be covered by a membrane to which an

* Epist. 83, in Opp. i. p. 463, 482. Anat. et Contemp. p. 52 in Opp. ii. Ibid. p. 27. Contin. Arcan. p. 17 in Opp. ii.

† Of Microscopes, &c. vol. i p. 128.

‡ P. 214, seq.

oscillatory motion was communicated by the agitation of the globules underneath it. He perceived the motion in question in no part but the labial appendages, and he imagined it to be connected with the male generative function, of which he therefore conceived the parts mentioned to be the organs. It is obvious that the appearance seen by Ehrman was the undulating motion of the cilia, which organs, however, he had not recognised. He makes no mention of currents, and consequently could not perceive the connexion of the phenomenon with respiration, which was also less likely to occur to him, as he supposed the motion to be confined to the appendages mentioned.

The observations of Ehrman led Treviranus to investigate the subject;* and he distinguished two different motions, the one a muscular contraction, the other the peculiar motion alluded to by Ehrman. The latter motion had the appearance of a trembling or flickering of innumerable points, and seemed at some places as if produced by a moving fluid, and at others by the agitation of oblong vibrating organs. It was peculiarly distinct alongside each of the bars of the gills and appendages. He farther perceived that the agitation on the surface of these parts caused an eddying motion in the water in which they lay, and also set in motion globules of blood which had escaped from the vessels. On breaking down the parts into small fragments, he found that each retained its power of motion, by which they moved in most manifold directions, the larger masses at the same time contracting and dilating themselves. From these observations Treviranus concludes that the bivalve Mollusca afford an example of a structure in which the integrant parts possess an independent vitality. Their independent vitality shews itself in the persistence of their automatic motion after solution of organic connexion with each other, and this motion is intermediate in its nature between the spontaneous movements of organic molecules in infusions, the male semen, &c. and the motion of muscular parts, which requires the integrity of the texture and the application of a stimulus. These reflections on the relation of the phenomenon to the general laws of organization are the sole inferences which he draws from his observations. He notices the motion of the water only as a concomitant and subordinate circumstance, not having been aware of its determinate direction, its relation to the respiratory process, or, in short, of its being the chief end and effect of the motion of the cilia.

The next researches on the subject are those of Huschke, narrated in a paper in the Isis for 1826.† Not having seen the original, we must content ourselves with a brief notice of them to be found in Burdach's Physiologie.‡ It is there stated that on detaching a portion of the gill of the Fresh-water Mussel (*Unio pictorum*), Huschke found that the water " moved upwards on one side, and then in an eddying manner back again."

* Vermischte Schriften, Band iii. p. 234.
† P. 623.
‡ Band iv. p. 434.

Raspail, in a memoir on a species of fresh-water polype, published in 1828,* pointed out the analogy between the phenomena exhibited by the gills of Mollusca and those observed in infusory animalcules and polypi.

Ciliary currents were now described by various other writers of eminence, but their causes were very commonly mistaken: among the number may be quoted Poli,† Delle Chiaje,‡ Carus,§ De Blainville,‖ and Unger.¶

Having observed currents produced in other instances by an impelling power inherent in the surfaces over which the fluid passed, I was myself led to suspect that the respiratory current in bivalve Mollusca was of the same kind, or that it was caused by an impulsion communicated to the water by the surface of the gills and other parts over which it was conveyed in its passage, without being aware of any similar view having been entertained by others. I then observed the determinate direction of the impulsion along the surface, together with the arrangement and action of the cilia. These observations were published at the time (1830) in a paper already mentioned,** in which also the respiratory currents of the bivalve Mollusca are considered as a particular example of a more generally prevailing phenomenon.

In a paper on the circulation of the blood, in Magendie's Journal for 1831,†† there are some remarks pertaining to the present subject, from which it appears that the author, M. Guillot, had observed the ciliary motion of the gills of the Sea-mussel and Oyster. He has, however, like Baker, mistaken the regular undulations of the cilia for the circulation of a fluid within vessels. He takes no notice of any motion or current excited in the water.

Carus,‡‡ in a memoir on the development of the River-mussel, states that he observed an undulatory or oscillatory motion of the gills, and that by this motion, which he conceives to be in the substance of the gill, the water is propelled, and the general respiratory current through the branchial cavity produced. It is obvious that what he calls an oscillation of the substance of the gill, and which he erroneously supposes has previously escaped attention, is merely the undulatory motion of the cilia.

The last researches on this subject which we have to notice are those of Purkinje and Valentin.§§ As above stated, they discovered the ciliary motion in the alimentary canal of the Mollusca, having found it in the Lymnæa, Paludina, and the Fresh-water mussel.

* Mémoires de la Soc. d'Hist. Nat. de Paris, tome iv. p. 131, seq. Chimie Organique, 1833, p. 246.
† Testacea utriusque Siciliæ, t. i. 51.
‡ Istituz. di Notom. e Fisiolog. comp. t. i. p. 278.
§ Lehrbuch der Zootomie.
‖ Malacologie, 157.
¶ Uber die Teichmuschel, p. 10.
** Edin. Med. and Surg. Journal, vol. xxxiv.
†† Tom. xi. p. 182.
‡‡ Nova Acta Acad. Cæs. Leop. xvi. p. 58, seq.
§§ Loc. cit.

Such is an outline of the observations hitherto made relative to the ciliary motion in the bivalve Mollusca. We may now shortly consider those which refer to the other classes of these animals.

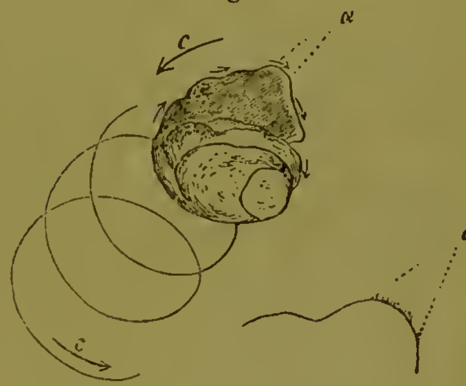
Dr. Fleming,* in describing the cilia in some species of Polypi, states that "analogous hairs" exist on the branchiæ of the Tritonia, which may probably be considered as forming part of the aerating organs. He also mentions, in another place,† that these branchiæ "readily fall off, and, as if independent, are capable of swimming about for a short time in the water, by means of minute hairs with which their surface is covered, and which move rapidly, pushing forwards the distal extremity." Gruithuisen, as formerly mentioned, observed the ciliary motion, and recognised its true nature in the Valvata branchiata, a species of fresh-water snail. Also Raspail,‡ having seen the phenomena produced by the gills of the Fresh-water Mussel, was led by analogy to discover the same in the Lymnæa and Paludina. Without being aware of these previous researches, I observed the ciliary motion in several different tribes of marine Mollusca, and shewed that it prevailed extensively among Mollusca generally. Mr. Lister, as has been already stated, has subsequently discovered that it exists in the Ascidia; and since then I have also found it in that animal, though in a different species.

9. *Of the ciliary motion of the embryo of Mollusca.*—The embryo of Mollusca exhibits, while within the egg, a peculiar rotatory motion which belongs to the class of phenomena we are here considering, and is referable to the same cause. This motion has been observed in the Gasteropodous and Bivalve Mollusca, and may perhaps be found in others.

Gasteropoda.—Swammerdam§ states that in examining the young of the viviparous water-snail, while they were yet inclosed in the membranes of the ovum, he observed the embryo turning round in the contained fluid with considerable rapidity, and, he adds, "in a very elegant manner." He again mentions the fact in another place.‖ Baker observed the same appearance in the ova of a fresh-water snail, which appears to have been the common Lymnæa. He says,¶ "when the eggs are about a week old, the embryo snail may be discerned in its true shape, turning itself very frequently within the fine fluid in which it lies." These brief notices of this remarkable fact by Swammerdam and Baker seem to have failed to excite the curiosity of succeeding naturalists, for there would appear to be no account of any subsequent researches on the subject till those of Stiebel published in 1815,** who seems not to have been aware that the fact had been previously noticed. Stiebel's observations were made on the ova of the Lymnæus stagnalis. They were followed by those of Hugi* in 1823, and Carus in 1824,† on the same species, to which Carus afterwards‡ (in 1827) added corresponding observations on the Paludina vivipara. About the same time (1827) Dr. Grant extended the inquiry to salt-water Gasteropoda, both naked and testaceous, and, as far as I know, was the first to point out the cilia, which are very conspicuous in salt-water species, as the agents which cause the rotation.

The eggs of the Lymnæus (or Lymnæa) are deposited in clusters, being imbedded in oblong masses of gelatinous matter that are found adhering to stones or water-plants. Each egg consists of an oval pellucid membrane, containing within it the yolk surrounded by a considerable quantity of limpid fluid. The yolk is at first round, without any obvious distinction of parts, but in the progress of development it changes its figure, and is gradually converted into the embryo, of which the shell and several principal organs can soon be distinguished. From the descriptions of the authors above mentioned, as well as from some observations made by myself, it appears that the embryo is at first motionless, but that as soon as the distinction can be perceived between the anterior or cephalic extremity and the rest of the animal, its rotatory motion commences. This invariably goes on in the manner indicated by the larger arrows (*c*, *c*) in the annexed figure, the head or anterior extremity

Fig. 19.



Embryo of Lymnæa.

continually receding. After a time the rotation is combined with a progressive motion, by which the embryo, while turning on its axis, moves onwards at the same time along the inside of the egg, performing a circuit like a planet in its orbit. The path described by a point on the surface is indicated by the spiral line in the figure.

Stiebel, as well as the earlier observers mentioned, is silent as to the cause of this curious phenomenon. Carus§ at first denominated it a primitive or cosmic motion, without clearly

* Mem. of Wern. Soc. of Edin. iv. p. 488.
† Philosophy of Zoology, v. ii. p. 470.
‡ Loc. cit.
§ Biblia Naturæ, p. 142.
‖ Op. cit. p. 179.
¶ Of Microscopes, &c. vol. ii. p. 325, 329.
** Diss. sist. Lymnæi stagnalis anatomen, Goetting, 1815, and Meckel's Deutsches Archiv für die Physiologie, Bd. i. p. 424. Bd. ii. p. 557.

* Isis, 1823, p. 213.
† Von den äussern Lebensbedingungen der weiss-und kaltblütigen Thiere. Leipz. 1824.
‡ Nova Acta Acad. Cæs. Leop. vol. xiii. p. 763.
§ Von den äuss. Lebensb. p. 59.

explaining what he meant by the term. Having subsequently discovered that a current existed in the fluid in an opposite direction to that followed by the embryo, he ascribed the motion to an attraction and repulsion exerted by the substance of the embryo on the surrounding fluid,* more especially at the region of the body where the respiratory organ was afterwards to be developed, and justly conceived that the chief purpose served by it was to renew the water on the respiring surface of the embryo. The attraction and repulsion again he supposed to be produced by an oscillatory motion which he perceived on the surface of the embryo. This oscillatory motion, although he describes it as taking place in the substance of the animal, seems to be nothing else than the usual undulatory play of moving cilia, such as has been already described in other instances,—indeed he himself compares it to the undulation on the arms of polypi. I have distinctly perceived the cilia, though they are very small, in the embryo of the small species of Lymnæa common in this country. It is the one represented in the figure, but considerably magnified. The current takes place along the whole of the surface indicated by the small arrows, which also mark its direction, being opposite to that in which the embryo moves. The cilia, though they probably exist over all this surface, were distinctly seen only on the part inclosed between the dotted lines at *a;* it required a doublet of one-thirty-fifth of an inch focus to make them visible.

Appearances similar to those described were discovered by Dr. Grant in the ova of Marine Gasteropoda. In examining the embryos of the Buccinum undatum and Purpura lapillus, which are inclosed in groups within transparent sacs, he was struck with a rapid and incessant motion of the fluid in the sac towards the fore part of the embryo, and he observed that this motion was produced by cilia placed around two funnel-shaped projections on the fore part of the young animal, which form the borders of a cavity in which he perceived a constant revolution of floating particles. He also observed these circles of cilia in the young of other testaceous Mollusca, as the Trochus, Nerita, &c. in which the embryo was seen revolving round its axis. He met with the same appearance in the naked Gasteropoda, as the Doris, Eolis, &c. The embryo of these revolves round its centre, and swims rapidly forward by means of its cilia, when it escapes from the ovum. My own observations on the ova of the Buccinum agree generally with those of Dr. Grant. The larger cilia are placed round the prominent border of a cavity on the fore part of the body, but the surface of the foot and other neighbouring parts is also ciliated, though the cilia are there much smaller. Dr. Grant assigns various uses to these motions; it seems not to have occurred to him that they were connected with respiration, although there can be little doubt that they are principally subservient to that function.

* Nova Acta, xiii. p. 771.

Acephala.—The rotation of the embryo of bivalves was discovered by Leeuwenhoek, and described by him in one of his epistles, dated October, 1695.* On examining the ova of a species of Fresh-water Mussel with the microscope, he observed the embryo turning slowly round within the egg, like a sphere revolving on its axis. This was at a time when the shell could be distinctly perceived on the young mussel; he had failed in discovering the phenomenon in some ova of the same species which he had examined at an earlier period of advancement.† He adds, that he was so much delighted with the spectacle of the young Mussels turning round within the egg, that he spent two hours along with his daughter and his draughtsman in contemplating it. Baster,‡ who wrote in 1762, seems to have observed an appearance of the same kind in the ova of the Oyster, if we may judge from a reference by Cavolini, for I have not been able to consult the original. More recently (1827) Sir E. Home and M. Bauer§ perceived the motion in the embryo of the Fresh-water Mussel, as described by Leeuwenhoek, but erroneously attributed it to a small worm which pierces the egg and preys on the young mussel, and which, according to their view, by dragging on it pulls it round in the manner described. Lastly, Carus subjected the phenomenon to a more careful investigation, in the course of his researches on the development of the River Mussel.|| According to his observations the embryo, at the time the motion becomes perceptible, has acquired a flattened triangular shape (*fig.* 20), the two halves of the shell cover its two surfaces, and are united together by the hinge at the base of the triangle. When the ovum is placed under the microscope, the embryo is seen moving round in a horizontal direction, as indicated by the larger arrows, appearing as if it turned on the centre of the lowermost shell. When the embryo is extracted from the egg, a current is perceived in the water opposite that part where the current enters and issues in the adult animal, (as shown by the small arrow,) and Carus therefore attributes its rotatory motion to an attraction and repulsion exerted on the water by that part of the embryo, which is afterwards to form the respiratory organ. The attraction and repulsion of the water he supposes to be produced by an oscillatory motion observable in the substance of the animal at its surface, as in the embryo of the snail, which motion, as we have already seen, is in reality an undulatory movement of minute cilia. As in the snail also, he conceives the phenomenon to be connected with respiration. For an account of his

Fig. 20.

Embryo of Mussel.

* Ep. 95. Cont. Arc. Nat. 1697, p. 26, 27, in Op. tom. ii.

† Ibid. p. 20.

‡ Opuscula Subseciva, tom. ii. p. 146.

§ Phil. Trans. 1827, p. 39.

|| Nov. Acta, xvi. p. 27, sqq.

observations on the velocity and direction of the motion, and its supposed influence in determining the figure of the animal, I must refer to the paper itself.

The analogy of these motions of the embryo of the Mollusca with the phenomena exhibited by the ova of Infusoria, Polypi, Sponges, and Actiniæ, already described, scarcely requires to be pointed out. We shall afterwards see that it extends to the ova of Batrachian Reptiles.*

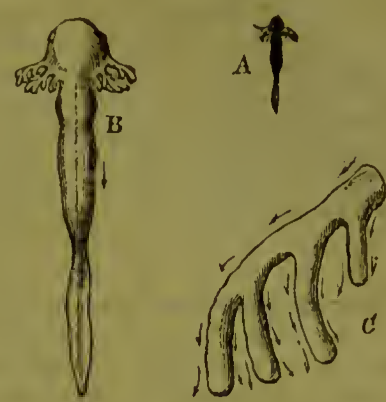
11. *Phenomena of the ciliary motion in the Vertebrata.*—The ciliary motion exists very extensively in vertebrated animals. Until lately it had been found only in the larvæ of Batrachian Reptiles, but Purkinje and Valentin† have recently made the important discovery that it exists also in adult Reptiles, Birds, and Mammiferous animals; and it seems to prevail generally throughout the three classes, having been found by these naturalists in all the numerous examples of each class examined by them in the course of their investigations. It has not been found in Fishes, though many species have been submitted to examination.‡

The parts of the body which exhibit the ciliary motion in the Vertebrata are, the lining membrane of the respiratory organs, and that of the generative organs in the female. Besides this general situation, it is found on the external gills and surface of the body in the larvæ of Batrachia, and on the surface of the embryo of these reptiles while contained within the ovum.

A. *Reptiles.*—The ciliary motion has been discovered in all the orders of Reptiles. It has been found in every species submitted to examination, and is therefore presumed to exist in all.

Batrachian Reptiles. 1*st.* *Larvæ and ova.*—The Batrachian Reptiles, while in the fœtal or larva state, breathe by means of gills or branchiæ, and it was on the gills of the young Salamander and Frog that the phenomenon under consideration was first discovered as existing in vertebrated animals. The gills of the young Salamander might in appearance be compared to feathers or pinnated leaves; there are three on either side, each consisting of a main stem bearing two rows of simple leaflets; they are wholly external, projecting backwards and outwards from the side of the neck. The tadpole of the Frog (*fig.* 21) has at first gills resem-

Fig. 21.



Larva of Frog.

bling those of the Salamander, but of a simpler form; they are also three on each side, but have each only five or six diverging branches. The gills of the Salamander, although not permanent, endure till the animal makes full use of its lungs, but the external gills of the Frog are of very short duration, being soon superseded by internal gills, more resembling those of a fish, with which the animal respires for the rest of the larva state.

By means of the microscope the blood may be seen circulating through the external gills of the Frog and Salamander; it passes outwards to their extremities by the branchial arteries, and returns in a contrary direction by the branchial veins. The water also is moved continually over these organs, for the purpose of respiration, in a constant and determinate direction, and this is effected by the peculiar impelling power we are here considering, viz. the ciliary motion on their surface.

Steinbuch,* a German naturalist already mentioned, while examining the circulation of the blood in the gills of the Salamander, observed that small bodies floating in the water were carried, as if by attraction, to the surface of the gill, and again repelled from it. He also found that portions detached from the gill moved themselves through the water, or if kept fixed, continued as before to attract and repel small objects in their vicinity. From these and similar facts he was led to conclude that the water was continually propelled over all parts of the gill, that the current thus produced served to renew the water in the process of respiration, that the power producing the propulsion resided in the gill, and was exercised independently of the will of the animal; and lastly, from the analogy of Infusoria and Polypi, in which currents are produced by cilia, he inferred that in this case also the water was probably impelled along the surface by the action of cilia, though he could not actually perceive any such organs. Steinbuch next examined the tadpole of the Frog, and found that its ex-

* In the preceding account of the ciliary motions in the *Invertebrata* no mention has been made of their existence in the class Crustacea: I think it necessary to state that I have examined this class, but without success; and since these pages have been put into the printer's hands I have re-examined the crab and lobster with the greatest care, all the respiratory and alimentary surfaces, the inner surface of bloodvessels, &c. with lenses of all powers, but without finding the phenomenon. I suspect the respiratory currents in Crustacea which are produced by the motion of the branchiæ themselves, or of the plates or oars with which many are provided in order to renew the water, have been confounded with the currents produced by cilia, more especially as many of the organs employed for the purpose in the *Crustacea* are fringed with long hairs; but I would scarcely reckon such motion as ciliary any more than those occasioned by the gill-covers of a fish.

† Müller's Archiv. 1834. Edinb. New Philos. Journal, xix. and Comm. Phys. de Phenomeno motus vibratorii continui. Wratislav. 1835, 4to.

‡ See note at p. 29.

* Analekten neuer Beobachtungen und Untersuchungen für die Naturkunde, Furth, 1802. p. 46, sqq.

ternal gills exhibited the same phenomena, but he could discover nothing of the kind on the internal gills.

Gruithuisen* observed in the tadpole of the Green Frog that so soon as the circulation of the blood began in any part of the gills, small objects were attracted and repelled from that spot, and that the same took place a few days later on the tail wherever vessels had been formed. He conceived that the motion of the water was for the purpose of exposing the blood to its influence, and compared it to the current produced by Infusoria by means of cilia. He does not say, however, that he had seen cilia in the tadpole.

Huschke† observed that the water in the vicinity of the gills of the young Salamander was thrown into a boiling-like motion, while it flowed steadily at other parts of the body.

Without being aware of these previous discoveries, I was led in 1830, by an accidental observation of my own, to go over nearly the same ground.‡ I had cut off one of the external gills of the tadpole of the Frog, and placed it with a drop of water under the microscope, with the view of measuring the size of the globules of blood that might flow from it, and was astonished to perceive that the globules, on escaping from the cut part of the gill, moved rapidly along its surface towards the points of the branches in a constant and uniform manner. On further inspection it soon became evident that the blood-globules were entirely passive in their motion, and that other light particles brought near the gills were moved in a similar manner; their motion being manifestly owing to a current produced in the water along the surface of the gill in a determinate direction. A conclusive proof of this was afforded by putting the gill which had been cut off, into a watch-glass with a larger quantity of water. It was then seen that when the gill happened to be fixed by any obstacle, small bodies in its vicinity were moved along it as before towards the points of the branches, but when unimpeded the gill itself advanced through the water in a direction contrary to that in which the particles were moved, the trunk being turned forward; the tendency to produce a current in one direction, thus causing the gill, now no longer fixed, to move in the opposite one. The current began at the root of the gill, and ran along the branches, at the points of which it did not continue its primitive direction, but turned off sideways, and immediately ceased. (See *fig.* 21, C).

I soon found that the gill was not the only part of the animal which excited motion in the water. Nearly the whole surface of the body produced the same effect. A general current commenced on the fore part of the head, proceeded along the back and belly and the two sides, to the tail, along which it continued to its extremity. It was not so strong as that on the gills, but agreed with it in other respects.

I continued for some time to observe the phenomenon in the larva of the Frog, in order to find out whether it underwent any alteration in the progress of the developement of that animal. It is known that after a time the external gills become covered by a fold of the skin, and inclosed in the same cavity with the internal gills, when they gradually shrink and at last disappear. On examining the animal while this change was taking place, and for some time after, it appeared that the external gills after their inclosure still retained their peculiar property, and continued to do so as long as any portion of them remained; the current on the body remained the same; on the tail it acquired a twofold direction diverging from the middle part or continuation of the vertebral column, obliquely upwards and downwards towards the upper and lower edge. As the animal advanced in growth, the currents gradually disappeared over the greater part of the surface, continuing longest at the posterior part of the body; at length, when the posterior extremities were so far advanced in growth that the thigh, leg, and toes could be discerned with a magnifying glass, which was the latest period of observation, the current existed only at the commencement of the tail, and on a small part of the body near the hind leg. The internal gills, though tried in various stages of development, did not exhibit the phenomenon.

I next sought for the same appearances in the larva of the Newt or Water Salamander, which was first examined a few days after its exclusion from the egg when its gills are very simple. At this period the surface of the animal produces currents agreeing in almost every circumstance with those which take place in the larva of the frog at a corresponding stage of its development. Particles of powder diffused in the water are carried along the surface of the body from before backwards; on the gills they are conveyed along each of the trunks from the root to the extremity. The gills also, when cut off, move through the water with the cut extremity forwards, in a direction contrary to the currents. I have since found nearly the same phenomena in the gills at a much later period.

It was evident that the purpose of these currents was to effect a renewal of the water on the respiratory surfaces; respiration in these animals probably being performed not only by means of the gills, but also by the general surface of the body.

It appeared that the power of impelling the water was wholly confined to the external surface of the animal; a portion of the skin being raised and detached, floating bodies were moved along its external surface only. Parts cut off from the animal continued to excite currents for several hours after their separation, and the smallest portion produced that effect. In these cases the current always moved in the same direction relatively to the surface of

* Salzburg. Medicinisch-Chirurgische Zeitung, 1819, ii. p. 447.

† Isis, 1826, p. 625, (cited in Burdach's Physiologie, from which I quote, not having seen the original.)

‡ Edinb. Med. and Surg. Journal, xxxiv.

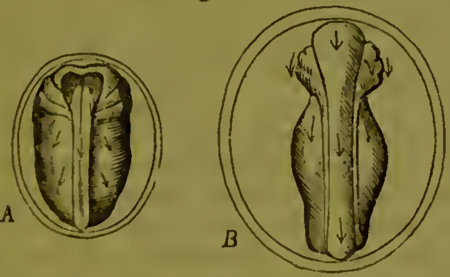
the detached parts, as it had done previous to their separation.

At the time of making these observations I had not been able to detect Cilia in these larvæ, although, from the analogy of the Invertebrata, I was led carefully to look for them. Since then I have succeeded in perceiving them with the aid of Wollaston's doublet of one-thirtyfifth of an inch focus, especially when a portion of the gill is compressed under a plate of mica. They are to be distinguished chiefly by their waving motion, which is so characteristic as to remove all doubt of their existence; though here, as in other instances in which they are very minute, it is not always possible to demonstrate their existence by actual observation on every spot of the surface.

Ova of the Batrachia.—In the course of the above-mentioned observations, I was led to enquire whether the phenomena in question appeared at a still earlier stage. With this view I examined the ova of the Newt, which for a considerable time may be procured in all degrees of advancement, and found that the ciliary motion presented itself in the embryo a considerable time before its exclusion from the egg. Since then I have observed the same with regard to the embryo of the Frog.

In both cases the embryo is formed from the yolk or opaque central part of the ovum, by a series of changes sufficiently well known; it is surrounded by a clear fluid, which is inclosed between it and the external pellucid membrane of the egg. By means of a lens, minute bodies may generally be perceived floating in the fluid, which by their motion serve to indicate the currents that take place in it; but with a little care the embryo may be extracted from the egg, and then the course of the currents along its surface can be rendered more evident by the usual means. A (*fig.* 22) is an enlarged view of the embryo

Fig. 22.



Embryo of the Frog.

of the Frog at the earliest stage at which I have detected the motion. The vertebral canal is just closed, and at the fore part of the body three ridges on each side indicate the commencement of the gills. The arrows point out the course of the currents. They proceeded backwards along the dorsal surface, diverging in a direction downwards and backwards on the sides. They were visible but weaker on the abdominal surface. B represents the embryo farther advanced, the currents have nearly the same direction but are better marked, they are strongest on the lateral eminences of the head which correspond to the future gills. In the embryo of the Newt, the phenomena are in a great measure similar; the currents seemed, however, to begin and to continue most vigorous on the abdominal surface; they are more particularly described in the paper referred to.

On extracting the embryo of the Frog, and viewing its surface in profile with Wollaston's doublet, moving cilia may be perceived on various parts. They appear like a transparent undulating line on the surface, and, though very minute, are so distinct as to leave no doubt of their existence.

No one can fail to perceive the analogy which subsists between the phenomena just described, and those which occur in the ova of Zoophytes and Mollusca. I have not been able distinctly to perceive a rotation of the embryo of the Batrachia, as observed in the other instances, but Purkinje and Valentin state that they have seen it, and Rusconi observed that the embryo of the Frog, when extracted from the ovum, turned round in a certain direction, which motion he supposed to be produced by water entering and issuing through pores in the skin.*

The phenomena in the Batrachian larvæ have since been observed by Müller,† Raspail,‡ and Purkinje and Valentin.§ The last mentioned naturalists also distinguished the cilia and perceived the motion within the egg.

Adult Batrachia.—The ciliary motion was discovered in the adult Batrachia by Purkinje and Valentin; indeed, it may not be improper again to state that the discovery of the phenomena in adult Reptiles generally, and in Birds and Mammiferous animals, is due to these physiologists.

According to their account, the ciliary motion in the Batrachia, as well as in all other vertebrated animals in which they have discovered it, occurs in two situations within the body, viz. on the lining membrane of the respiratory organs and on that of the genital organs of the female. They state that it exists over the whole internal surface of the lungs, and in the nose, mouth, and pharynx, extending as far back in the throat as the glottis, but no farther. They say nothing of the direction of the impulsion. Again, in the female, they discovered the motion on the internal surface of the oviduct. The result of my own examination of the Newt, Frog, and Toad is somewhat different. In all the three I found the ciliary motion very distinct in the mouth, throat, and gullet; in none could I perceive it in the lungs, notwithstanding very careful trials. In regard to the oviduct I have examined it only in the Newt, and although I could perceive something like the motion on the edges of its superior orifice, I could not detect it on the internal surface of the tube.||

* Sur le Developpement de la Grenouille Commune. Milan, 1826.

† Burdach's Physiologie, Bd. iv. p. 434.

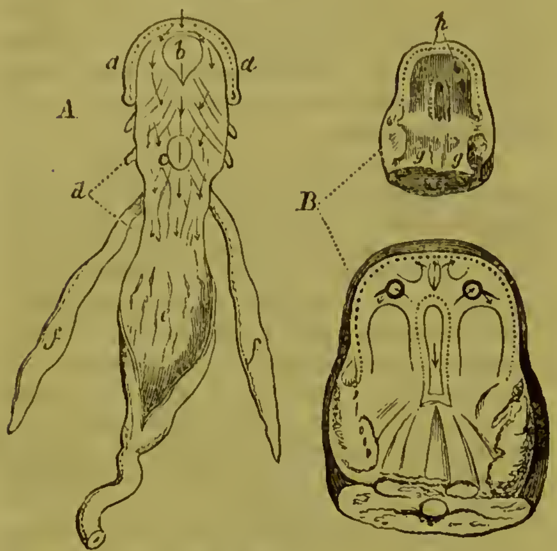
‡ Chimie Organique, 1833, p. 250.

§ Op. cit.

|| Edin. New Phil. Journal, xix.

The ciliary motion in the mouth and throat occurs all the way from the opening of the mouth to the termination of the œsophagus. Its extent and the direction of the impulsion are easily ascertained by means of powdered charcoal; they are pointed out by the arrows in the adjoining figures, A and B (*fig.* 23),

Fig. 23.



Salamander.

which are taken from the Newt, the appearances in the Frog and Toad being not materially different. *a* is the lower jaw detached from the head, *b* the tongue, *c* the glottis, *d* the œsophagus cut off from the head (at *g*, *g*, *fig.* B), and laid open from above, *e* the stomach, and *f*, *f*, the lungs. The general course of the impulsion, or, if in this case we might so express it, the currents, is longitudinal; they begin at the symphysis of the lower jaw and extend to the lower end of the œsophagus, where they terminate abruptly at the entrance of the stomach, thus differing from the description given by Purkinje and Valentin; but it is worthy of notice that these observers describe the motion in the Tortoise and Serpent as extending the whole length of the œsophagus. At particular parts the impulsion follows the direction of the plaits of the lining membrane. Figure B represents the head and the roof of the mouth, from which the lower jaw has been separated. On this part of the mouth also the general course is longitudinal, from before backwards; at the nostrils *h*, *h*, the particles are drawn in at one edge and issue at the other, as indicated in the outline of figure B.

As regards the use of the ciliary motion on the internal membranes of the Batrachia, we can scarcely doubt that one purpose is to convey onwards the secretions of these membranes in the direction indicated. It is not impossible also that it may have some more intimate connection with the respiratory process; but on this point we have not as yet sufficient grounds for forming a probable opinion.

Sauria, Ophidia, and Chelonia.—The authors mentioned describe the appearances in these reptiles as being similar to what they have found in Batrachia. The ciliary motion occurs in the oviduct and in the nose, mouth, pharynx, Eustachian tube, and inner surface of the lungs. In the Serpent and Tortoise they state that it extends along the gullet to its termination at the stomach, as we have seen to be the case in the Batrachia. The motion of the cilia is remarkably vivid in the mouth of the Serpent, and in the Tortoise it endures for several days after death, not ceasing till the parts are destroyed by putrefaction.

B. *Birds.*—The same physiologists have discovered the phenomena in thirteen species of Birds, belonging to five different orders; and as they met with it in every species submitted to examination, they infer that it exists in all.

In Birds, as in other Vertebrated animals, the motion shows itself on the lining membrane of the oviduct and that of the respiratory organs. It was detected in the nasal cavities and Eustachian tube, in the windpipe and its divisions, even in the smallest branches capable of investigation, and on the internal surface of the large sacs or receptacles into which the air penetrates. No trace of it could be found in the mouth and pharynx. In regard to the direction of the impulsion, the authors state that in the oviduct they had found it to be from the internal towards the external extremity of the tube, and in the windpipe from its orifice towards its branches, or from without inwards, at least they so observed it once in the domestic Fowl. The phenomenon exists in the fœtus of the bird, having been distinctly seen in the fœtal pigeon near the full period.

C. *Mammalia.*—An accidental observation led Purkinje and Valentin to discover the ciliary motion in Mammalia, and they followed out that discovery by extending their inquiries to other vertebrated animals. While examining the Fallopian tube of a rabbit that had been recently impregnated, in order to discover the ova, they chanced to observe small portions of the mucous membrane of the tube turning round, and moving briskly, and recognized the appearance as an instance of ciliary motion. The whole uterus and organs of generation generally were then diligently searched, and these motions were discovered throughout their entire extent, though of very different degrees of intensity in different places. They were particularly brisk in the tubes, less so in the cornua of the uterus, still less in the conjoined parts of the organ, most lively of all on its swollen and dark red lips, and of considerable strength in the vagina. After finding the same appearances in the oviduct of Birds and Reptiles, they succeeded also in discovering it in the lining membrane of the air-passages in all the three classes. In Mammalia the ciliary motion of the respiratory organs occurs on the mucous membrane of the nose and its sinuses, and that of the Eustachian tube, also on the lining membrane of the lower part of the larynx, the trachea, and bronchial tubes, extending to their smallest divisions capable of examination. No trace of it can be found in the glottis, nor

in the mouth and pharynx. It was also sought for unsuccessfully in the lachrymal passages.

The authors mentioned have now examined it in twelve species of Mammalia, and have found the same appearance in all of them; they add that, although they have had no opportunity of inspecting the parts in the human body so soon after death as to see the cilia in motion, yet by covering the surfaces to be examined with blood, which preserves the appearance longer than any other fluid, they were able on examination, thirty hours after death, satisfactorily to distinguish the cilia both in the nose and windpipe.

I have seen the phenomena in the nose, trachea, and Fallopian tubes of the Rabbit, and in the trachea of the Dog.*

According to Purkinje and Valentin the motion occurs in the uterine mucous membrane, both in the impregnated and unimpregnated state; but in gravid animals it appears only on those parts of the uterus which are not adherent to the chorion or external envelope of the fœtus. The direction of the impulsion they state to be from the internal extremity of the tube, towards the orifice of the vagina. It seems wanting on the genital membrane of young animals. On the other hand, it occurs in the respiratory passages of the fœtus, it was detected in fœtal calves and lambs, and in fœtal pigs not more than two inches long. The authors could not with certainty distinguish the direction of the impulsion in the air-passages of Mammalia. In some parts of the nose of the Rabbit, I have been able to trace it clearly enough by means of charcoal powder, the parts being placed in tepid water. On the inferior turbinated bone the grains of powder were slowly carried forwards, following the direction of the projecting laminæ of the bone. On breaking open the maxillary sinus and trying its lining membrane in the same way, the impulsion seemed to be directed towards the back part of the cavity, where its opening is situated. By the same means I traced the direction in the windpipe of a young dog a few days old; the impulsion was best marked on the posterior part of the tube, and there it was obviously directed towards the larynx, the direction being thus different from what Purkinje and Valentin observed in the domestic Fowl.

PART II.

1. Summary of the animals in which the ciliary motion has been discovered.

From the foregoing facts it appears that the ciliary motion is a phenomenon which prevails most extensively in the animal kingdom, having been found in the highest as well as the lowest members of the Zoological scale. Among Vertrebated Animals it has been discovered in Mammalia, Birds, and Reptiles, viz. the *Batrachia*, *Sauria*, *Ophidia*, and *Chelonia*. Of the Invertebrata it has been found in Mollusca, viz. *Gasteropoda*, *Conchiferous acephala*, and *Tunicata*; in Annelida, viz. *Aphrodita*, *Arenicola*, and many *Tubicolar worms*, also in *Planariæ* and *Naiades*; in Echinodermata, viz. the *Asterias* and *Echinus*; in Actiniæ; in Medusæ; in Polypi; in Sponges; and in Infusoria. It is a remarkable fact that no trace of it has been observed in Fishes. I at one time supposed that the pendent filaments of the gills of the fœtal Skate and Shark might probably be found to exhibit it; but my friend, Dr. Allen Thomson, has carefully inspected those of the Skate without being able to perceive any appearance of it.*

2. Organs or parts of the body in which the ciliary motion has been ascertained to exist.

These may be referred to four heads, viz. the skin or surface of the body, the respiratory, alimentary, and reproductive systems. Its use in all these cases, or the function in general of the cilia, is to convey fluids or other matters along the surface on which the cilia are placed, or, as in the Infusoria, to carry the entire animal through the fluid.

a. Surface of the body.—Cilia have been found on different parts of the external surface, in Batrachian larvæ, in Mollusca, Annelida, Echinodermata, Actiniæ, Medusæ, Polypi, and Infusoria. Their function in this situation is various; in most cases it is evidently respiratory, but in many instances it is also locomotive, as in Infusoria and Medusæ, or prehensile, as in Infusoria and Polypi; and perhaps it is in some animals subservient to the sense of touch or smelling, as may be conjectured with regard to the cilia on the tentacula of some Mollusca.

b. Respiratory system.—The ciliary motion has been observed on the lining membrane of the air-passages of Mammalia, Birds, and Reptiles; and there, whatever may be its other uses, it at least serves to convey the secretions along the membranes, together with foreign matters, if any are present. It exists also on the external gills of Batrachian larvæ, and on the gills of Mollusca and Annelida. In other Annelida, in Echinodermata and Actiniæ, it is found on the external surface of the viscera and on the parietes of the cavity containing them, to which cavity the water has access. The pores and canals of the Sponge are probably both respiratory and alimentary passages, and under this head we must refer again to the cilia on the external surface of Medusæ, Polypi, and Infusoria, as belonging partly to the respiratory system. The use of the ciliary motion on the respiratory organs of animals with aquatic respiration is obviously to renew the water on the respiring surface.

c. Alimentary system.—The motion occurs in the mouth, throat, and gullet of Reptiles, in the entire alimentary canal of Mollusca, on

* Edin. New Philos. Journal, xix.

* Since the above was written, a short notice has appeared in "l'Institut" of 16th December, 1835, of the Transactions of the Leopoldine Academy for 1834-35, from which it appears that Purkinje and Valentin have at last succeeded in detecting the phenomenon in Fishes. They found it in the organ of smelling and the internal genital organs of the female. No further particulars are stated.

the internal surface of the intestine and cœcal appendages of the Aphrodita, within the stomach and cœca of the Asterias, in the stomach of the Actinia, in the canals of the Sponge, which no doubt belong partly to the alimentary system, and in the mouth, throat, stomach, and intestine of several Polypi. It is not easy to see the purpose of the motion in all these cases. In some it may merely convey secreted matters along the surface of the lining membrane; in Polypi it agitates the food within the alimentary cavity, and in several instances it seems almost to serve in place of ordinary deglutition, to carry food into the stomach.

d. Reproductive organs.—The phenomenon occurs on the mucous membrane of the Fallopian tubes, uterus, and vagina of Mammalia, and of the oviduct in Birds and Reptiles. From the direction of the impulsion being from within outwards, it is difficult in the meantime to assign any other office to the cilia in this situation than that of conveying outwards the secretion of the membrane, unless we suppose that it also brings down the ovum.

The phenomenon has been sought for in other parts of the body, but hitherto without success. Purkinje and Valentin state that on examination they could not find it in the following parts of vertebrated animals, viz. the skin, serous membrane, the alimentary canal, (except the mouth and gullet of Reptiles,) the gall-bladder, the biliary and pancreatic ducts, the urinary organs, the seminal vesicles and ducts, the conjunctiva, cornea, and iris, the internal surface of the bloodvessels, the globules of the blood and lymph, the chorion, amnion, allantois, and yolksac of Birds. I have also repeatedly examined the fœtal membranes of the common Fowl, and with the same result.

3. *Of the ciliary motion in the embryo.*—According to Purkinje and Valentin the ciliary motion of the genital mucous membrane does not appear in the fœtus, nor until the animals have made some approach to the adult state; that of the respiratory passages on the other hand becomes apparent in the embryo long before it attains maturity. The ciliary motion, however, to which we would here refer is that which occurs at a much earlier period on the surface of the embryo of many animals, and generally causes it to perform a rotatory movement within the ovum. It has now been observed in the ova of Batrachia, Mollusca, Actiniæ, Polypi, Sponges, and Infusoria. While the embryo is contained within the ovum, the cilia produce a current in a certain direction along its surface, or cause the whole embryo to move in the opposite direction; hence the very remarkable rotatory motion which occurs in many instances, and which is so well marked in the Snail. When it has escaped from the egg, the embryo moves about in the water by means of the cilia, as happens also with the naked gemmules of the Sponge after they are discharged from the parent. The ciliary motion is subservient to the respiration of the embryo, by renewing the contact of the water or fluid contained in the egg on the respiring surface, and in some instances, the Mollusca for example, the motion is observed to be especially strong at the part where the respiratory organ is afterwards developed. When the embryo quits the egg, the cilia serve also for locomotion, and by this provision the gemmules of fixed zoophytes are disseminated, and conveyed to situations suitable for their future growth.

4. *Figure, structure, and arrangement of the cilia in general.*—The cilia are best seen when their motion slackens; their shape, size, arrangement, and manner of moving may then be distinguished with tolerable accuracy, at least in the larger sort. Their figure is in general that of slender, conical, or sometimes slightly flattened filaments, broader at the base or root, and tapering gradually to the point. Their size differs greatly on different parts even of the same animal, but on corresponding parts of different individuals of the same species their size seems to be the same. The largest I have measured are those on the point or angle of the branchial laminæ in the *Buccinum undatum;* they are at least $\frac{1}{300}$ of an inch long. I have not attempted to determine the exact size of the smallest, but Purkinje and Valentin state it at 0.000075 of an inch, while they make the largest they have met with only 0.000908 in., which is considerably less than I have found them; but they had no opportunity of examining marine animals, in which, generally speaking, the largest cilia are met with. In the Sea-mussel the darker-coloured cilia are about $\frac{1}{1000}$ of an inch long, the others considerably less.

The cilia are very generally arranged in regular order. In some cases they are placed in straight rows, as on the gills of the Mussel; in others they form circles or spiral lines, as in many Infusoria; and Purkinje and Valentin state that in animals of the higher orders the most prevalent mode of arrangement is in spiral lines or ridges. They are generally set close together in the same row; on the gills of the Sea-mussel I find there are seven or eight of the larger cilia in the length of $\frac{1}{1000}$ of an inch, or about seven or eight thousand to the length of an inch, but in other cases there are many more. In some instances they are erect, or at right angles to the surface on which they are planted, in others inclined, and then it would seem that the inclination is in the direction of the currents which they produce. In some parts they are straight, in others curved, not only when in action, but also when at rest, and the points are bent in the same direction in which the currents flow.

The substance of the cilia is transparent, and for the most part colourless; in some, however, it is coloured brown or yellowish brown. It appears as if homogeneous, even when highly magnified, and no fibres or globules are distinguishable in it. It seems to vary somewhat in consistency, for the cilia on some parts appear extremely soft and pliant, and on others comparatively firm and elastic, though still abundantly flexible.

There is a peculiarity in the form of the cilia in some animals, of which the Beroë and other

Ciliograde Medusæ afford a good example. In these, in place of cilia of the usual form and arrangement, there are rows of broad flattened organs, each of which is made up of several simple filaments joined together by a common base, according to Eschscholz, or according to Dr. Grant by a connecting membrane in their whole length. The entire organ is raised or depressed at once, so that the filaments are all moved simultaneously, like the eye-lashes. The compound cilia in some of the Rotatoria, described by Ehrenberg, are probably of the same nature.

5. *Of the appearance of the cilia in motion.*—On examining these organs with a lens of $\frac{1}{33}$ inch focus, when their motion is not very rapid, the manner in which the individual cilia move may be distinguished with tolerable certainty. Most commonly they have a fanning or lashing motion, that is, the cilium is bent in one direction and returns again to its original state. The flexion takes place chiefly at the base or root, but not wholly there, for the rest of the organ is obviously bent and altered in figure; nay, the more elastic cilia, when their motion abates in intensity, appear sometimes to bend only near the point, the base and adjoining part remaining motionless.

When a number of cilia are affected in succession with this motion, the appearance of a progressive wave is produced, and as in such a case they are again and again moved in the same way at very short intervals, successive waves proceed along them in the same direction, which might be compared to those produced by the wind in a corn-field. Such at least seems to be the true explanation of the undulatory motion which so often occurs, although it must be confessed that the motion of the cilia individually cannot be distinctly seen when the undulation is most perfect. The undulations succeed one another along a range of cilia with great regularity, and except in the Rotifera, and perhaps some other Infusoria, they seem always to maintain the same direction in the same parts.

Purkinje and Valentin describe the motion of the individual cilia as being more frequently rotatory, or, as they term it, infundibuliform; and Ehrenberg states this to be the common mode in the Infusoria; the cilium describing a circle with its point, while the base is the centre of motion. From my own observation, however, I would be inclined to infer that this motion is by no means the most common.

6. *Duration of the ciliary motion after death and in separated parts.*—The continuance of the ciliary motion for some time after death, and the perfect regularity with which it goes on in parts separated from the rest of the body, are facts which have been already repeatedly stated, and sufficiently prove that the motion is quite independent of the will of the animal, and also that it is not immediately influenced by the circulation of the blood, even in the respiratory organs.

The time which it continues after death differs in different species of animals, and also, but in a much smaller degree, in different parts of the same animal. Its duration is influenced also by the temperature of the air, and by the nature of the fluid in contact with the surface. In Mammalia and Birds the period varies from half an hour to four hours, being longer in summer than in winter; but it is still further prolonged when the parts are covered with blood. In the gills of Batrachian larvæ I have seen the motion continue six hours; but of all vertebrated animals it is most enduring in the Tortoise, in which animal Purkinje and Valentin affirm they observed it fifteen days after death, when putrefaction was far advanced; the irritability of the muscles remained in the same animal for seven days. Among the invertebrata the River-mussel affords an instance of the great pertinacity of the motion, which ceases only when putrefaction has advanced so far as actually to destroy and dissolve the tissues.

7. *Effects of external agents on the ciliary motion.*—Steinbuch, Purkinje, and Valentin allege that on touching the parts, or giving them a gentle shock by merely striking against the object plate of the microscope, the motion is rendered brisker when it has become languid, or is even renewed in parts where it has ceased. They, however, attribute more importance to this fact than it seems to deserve; for it may be doubted whether the concussion in renewing the vivacity of the cilia does not act merely by removing obstacles which impede their play.

Electricity and galvanism produce no visible effect. A powerful discharge from a Leyden jar was made to pass through the River-mussel by Purkinje and Valentin without causing any change in the ciliary motion. Portions of the external gills of the Tadpole were subjected by myself to the same experiment and with a similar result, except when the surface was abraded, which occasionally happened with a strong discharge. I have exposed portions of the gill of the River-mussel while viewed with the microscope, to the influence of a galvanic battery of twenty-five pairs of three-inch square plates, charged with solution of salt, without being able to perceive the slightest effect on the motion of the cilia. The authors above mentioned obtained a similar result, both in the Mussel and the domestic Fowl.

The effect of temperature is different in warm and cold-blooded animals. In the former, according to Purkinje and Valentin, the motion stopped on exposure to a temperature of 43° F. while it went on at 54° F. On the other hand they found that in the Fresh-water Mussel it was not affected at 32° F.; and I found the same to be true of the Tadpole. A portion of the gills of the River-mussel, which I kept for five minutes in water at 96° F. shewed no change.

Acids, saline solutions, and other substances applied to the parts, differ in their effects according to the kind of animals submitted to experiment. Thus, for example, fresh water instantly arrests the motion in the Marine Mollusca, and also in other marine animals in which I have tried its effect, though a saturated solution of sea-salt destroys it both in salt and fresh-water species. Purkinje and

Valentin state the effects which they found to result from the application of various substances, but erroneously conceiving, from some preliminary trials, that the same substance produced the same effect in all animals, they confined their experiments to the Fresh-water Mussel. According to their experiments, which were made with a great many different substances, most of the common acid, alkaline, and saline solutions, when concentrated, arrest the motion instantaneously; dilution, to a degree varying in different substances, prevents this effect altogether, and a less degree of dilution delays it. The same is the case with alcohol, æther, aqua laurocerasi, sugar, and empyreumatic oil. Kreosote, muriate of baryta, sulphate of quinine, infusio pyrethri, and muriate of veratria, act less intensely. Hydrocyanic acid and watery solutions or infusions of belladonna, opium, capsicum, catechu, aloes, musk, gum-arabic, acetate of morphia, and nitrate of strychnia, produce no effect whatever. They accordingly infer that the substances affect the motion only in so far as they act chemically on the tissue.

The result of my own experiments differs from theirs in some points. In the River-mussel I found that hydrocyanic acid, containing ten per cent. of pure acid, invariably destroyed the motion. Solution of muriate of morphia, of medicinal strength, also arrested the motion in the Mussel, but not in the Batrachian larvæ. The motion on the gills of these larvæ also continues unimpaired in water deprived of air by boiling, or distilled, or impregnated with carbonic acid; a sufficient proof, it may be remarked, that it is independent of the chemical process of respiration.

In regard to the effect of animal fluids, the authors already mentioned state that bile arrests the motion, while blood has the property of preserving it much beyond the time that it lasts in other circumstances, at least in vertebrated animals; thus it continued three days in a portion of the windpipe of the Rabbit, which had been kept in blood. But it is singular that blood or serum, whether of Quadrupeds, Birds, or Reptiles, has quite the opposite effect on the cilia of invertebrated animals, arresting their motion almost instantaneously. Albumen and milk also possess the conservative property, though in a less degree.

8. *Effects of inflammation.*—Purkinje and Valentin excited inflammation artificially in the nose and vagina of rabbits, and are inclined to conclude from their experiments, which however are not numerous, that inflammation arrests the motion.

9. *Of the power by which the cilia are moved.*—It may next be inquired by what means or by what power the cilia are moved; and, in particular, whether their motion, like other visible movements in the animal body, is effected by muscular action.

Dr. Grant,* reflecting that in the Beröe a vessel conveying water runs beneath each row of cilia, and that, according to M. Audouin, in an allied genus of animals the water enters the cilia, is disposed to liken the motion of the cilia to that of the feet of the Echinodermata. He seems accordingly to think it probable that the cilia are tubular organs, which are distended and protruded by the injection of water into them from elastic tubes running along their base, in which the water is conveyed by successive undulations.

This view, however, seems scarcely reconcilable with the fact that the motion of the cilia continues in parts separated from their connexion with the rest of the body, portions so small that not more than two or three cilia are attached to them, and in which the operation of the supposed undulating tubes can scarcely be conceived.

Ehrenberg states that in the Infusoria he observed that the cilia were bulbous at the root, and that they were moved by small muscles attached to the bulb. Purkinje and Valentin also admit the existence of a bulb, and they conceive it likely that the cilia are moved either by muscular substance placed within the bulb, or by certain fibres which they believe they have discovered in the adjacent tissue. They describe these fibres as existing in the substance of the membranes or other parts supporting the cilia, being situated at the surface, straight and parallel, and appearing to be connected together by delicate cellular tissue; and they think it highly probable that they are of a muscular nature.

The whole phenomena of the ciliary motion seem to me most consistent with the notion that it is produced by muscular action. I must confess, however, that I have never seen the muscular fibres described, nor the bulbs; and perhaps the cilia are not moved merely by muscular fibres attached to their base, like the whiskers of the seal and cat, but may contain muscular substance throughout a greater or less portion of their length, by which they can be bent and extended; or perhaps they may in some instances be bent by muscular fibres, and resume their original shape and position by virtue of their elasticity.

We need not hesitate to admit that the ciliary motion is the result of muscular action on account of the smallness of the muscular apparatus necessary; for the researches of Ehrenberg on the Infusoria have brought to light examples of complex organization on as minute a scale as any here required. Nor need we hesitate on account of the great rapidity of action; for there are familiar instances of muscular motions of equal velocity. The continuance of the ciliary motion after death and in parts detached from the rest of the body, and its regularity in these circumstances, are appearances, startling at first, but which, though they differ in degree, may be fairly compared with those produced in similar circumstances by involuntary muscular action, and may be attributed to the same cause. Thus the different parts of the heart, which during life contract in a certain order independently of the will, continue to act in the

* Trans. of Zoological Society of London, vol. i. p. 11.

same regular order for a time, and in some animals for a long time, after death or separation from the body; and it is remarkable, although perhaps we are not warranted by observation to lay it down as a general rule, that there is a correspondence in the duration of the ciliary motion after death and the persistence of muscular irritability. In the Tortoise, for instance, in which it is well known that the irritability of the heart and other muscles endures remarkably long after death, the ciliary motion is also of extremely long continuance; while in Mammalia and Birds, the ciliary motion and muscular irritability are both comparatively soon extinguished.

On the whole, therefore, without laying any stress on the alleged discovery of a muscular apparatus by Ehrenberg and the other authors mentioned, we may venture to conclude that the facts known respecting the motion of the cilia are all reconcilable with the opinion that it is produced by muscular contractility.

10. Strange as it may seem, after what has been said, some observers maintain that the cilia have no real existence, even in cases where the appearance of them is the most perfect, and that the whole is an optical deception. I allude particularly to Raspail; according to him the water which quits the respiring surfaces has, in consequence of the change produced in it by respiration, acquired a different density, and consequently a different refractive power from the surrounding fluid; it therefore produces the appearance of lines or streaks at the surface of the parts, which streaks are the supposed cilia. It is scarcely necessary to repeat that the cilia are seen when at rest, when all motion of the water has ceased, and that they are evident in circumstances in which no interchange of materials can take place between the tissue and the water in contact with it; and indeed, after the details already given, it is needless to say more in refutation of this view.

11. *Of the motion caused in fluids by the cilia.*—One of the most remarkable characters of the motion produced in water and other fluids by the ciliary action, is its definite direction, which, except in some of the Infusoria, appears to be always the same in the same parts; at least I have never been able to perceive any exception to this rule. Appearances would rather lead to the belief that in the Infusoria the motion of the cilia is under the influence of the will, which would account for this and other possible cases of exception.

We have hitherto taken it for granted that the currents in the water are owing to the mechanical effect of the moving cilia, without formally adducing proofs in support of the opinion; but at the same time the details already given must have served as such. The currents cease when the motion of the cilia stops, they are strong and rapid when it is brisk, and feeble when it languishes; and though there are modifying circumstances or perhaps exceptions, yet in general the magnitude and velocity of the current seem to be proportionate to the size and activity of the cilia. It is true that while doubts remained as to the existence of cilia in several well-marked instances where the water unequivocally received its motion from the surface over which it flowed, and, independently of any visible contractions of the animal tissue, there was also considerable room to doubt whether, even in the cases where cilia were manifest, the effect of these organs was wholly mechanical, and whether the motion of the water was not rather due to some peculiar impulsive power in the tissue, differing from mechanical action. But more extended observation has almost wholly removed these exceptions, while it has considerably increased the number of conforming instances, insomuch that there seems at present no necessity for having recourse to any other explanation of the motion of the fluids than that it is produced by the action of the cilia, and that their action is the result of muscular contractility, a known property of animal tissues.

The phenomena of the ciliary motion seem therefore of themselves to afford no countenance to the notion of a peculiar impelling power of the animal tissue, in virtue of which fluids are visibly moved along its surface, independently of impulse communicated to them mechanically by cilia or by contraction of inclosing solids; nor am I aware of other facts which either alone, or viewed in connexion with the former, warrant such a notion. But as some physiologists believe in the existence of such a power, and found their opinion, at least partly, on alleged examples of visible motions of fluids in organized bodies, produced without cilia and independent of contraction of the solids, it may not be amiss here shortly to consider the principal facts which have been adduced as instances of this kind.

First, Three cases have been already mentioned in which currents, more or less resembling those produced by cilia, take place on surfaces on which cilia have not been detected; these are the currents in the Sponge, those of the Tubularia indivisa, and those within the stem and branches of Sertulariæ. In regard to the Sponge, it is true that cilia have been diligently sought for and without success; still, considering the difficulty of the investigation, it is not impossible they may exist in some part of the passages through which the water runs, though not yet discovered, especially as the ova possess evident cilia. With respect to the currents described by Mr. Lister within the stem of the Tubularia, it will be seen, on referring to the account of these, that farther observations would be required to settle the points here in question, viz. whether the floating particles receive their impulse from the surface over which they move independently of any contraction of the stem, and whether or not that surface is covered with cilia. To decide these points satisfactorily it would be necessary to lay open the tube and make trial of detached portions of the tissue as in other instances. The same remark is in a great measure applicable to the currents in the stem and branches of Sertulariæ. Indeed both

instances have been described above only because of their seeming analogy with the rest, but further investigation is still required to determine their true nature. Neither these, therefore, nor the Sponge afford unequivocal examples of the peculiar motion of fluids alluded to taking place independently of cilia. Of course we may pass over without notice the cases in which the appearance of the moving cilia has been mistaken for a circulating fluid,* or ascribed to other causes than the real one, and their existence erroneously denied.

Secondly, It is well known that in cold-blooded animals the blood continues to move in the capillary vessels for some time after the heart has been cut out. This motion for the most part goes on at first steadily from the smaller to the larger vessels in the arteries as well as the veins, and afterwards becomes oscillatory. Haller, who particularly investigated the phenomenon, was of opinion that it could not be attributed to contraction of the large vessels, to gravitation, nor to capillarity; he therefore attributed it to some unknown power which he conceived to be exerted by the solid tissues on the blood and also by the globules of blood on each other, and to this power, until farther investigation should elucidate its nature, he gave the name of attraction. The same opinion or a modification of it has been taken up by succeeding physiologists; accordingly many maintain the existence of a peculiar propulsive power in the coats of the capillary vessels different from contractility, or that the globules of blood are possessed of the power of spontaneous motion. Among others, Dr. Alison has adopted and extended this view in so far as he regards the motion of the blood in the capillaries as one of the effects produced by what he calls vital attraction and repulsion, powers which he conceives to be general attributes of living matter, or at least to manifest themselves in other processes of the living economy besides the capillary circulation.

The motion in question has certainly not been as yet satisfactorily accounted for by referring it to the operation of known causes. At the same time we can scarcely admit that the influence of such causes has been wholly avoided in the experiments in which the phenomenon has been observed. It is not impossible, for example, that a certain degree of agitation may be occasioned in the blood by the elastic resilience of the vessels reacting on it, after the distending force of the heart has been withdrawn. The necessity of the case therefore, though great, seems scarcely such as alone to warrant the assumption of a peculiar attractive or repulsive power acting on the blood at sensible distances, of whose existence in the animal economy we have as yet no other evidence. It may be remarked, finally, in regard to the phenomenon alluded to, that it cannot properly be termed a continuance of the circulation, for the blood does not necessarily preserve its original course, nor indeed any constant direction. (See CIRCULATION.)

Thirdly, In several plants motions have been observed in the fluids which are contained in their cells or vessels in determinate directions, and seemingly independent of any contraction of the parietes of the containing cavities. The best known example of this is in the Chara. Its jointed stem consists of a series of elongated cells, which contain a clear fluid with globules suspended in it. The globules are moved up one side of the cell and down the other in continual circuit. No contraction can be perceived in the parietes of the cells, which are indeed of a rigid texture, and this mysterious movement has therefore been ascribed to some unknown and invisible impelling power. It is doubtful, however, whether the motion can go on unless the cell is entire, the experiments of different observers on this point being contradictory, and it certainly has never been shewn that separated portions of the tissue continue to excite the motion. In this state of knowledge on the subject we can scarcely admit this or similar motions of vegetable juices as unequivocal examples of the operation of an impulsive power of the kind referred to; and even on the contrary supposition it does not follow that such a power exists in animals.

On the whole therefore, from what has been said regarding the several examples adduced, we may conclude that they do not afford unequivocal evidence of visible motions being produced in fluids in the animal body, independently of contractions of containing solids or of the action of cilia; and, consequently, that viewed in reference to the ciliary motion, they form no adequate reason for doubting that the fluid is moved mechanically by cilia.

I may conclude this article by observing, that though the general existence of the ciliary motion in the Animal Kingdom is already sufficiently established, yet many particular instances of it must still remain to be found out, especially in invertebrated animals; and whoever has opportunities and inclination to cultivate this field of inquiry will find his labour rewarded by much curious and interesting discovery.

* As by Baker, Guillot, and others.

THE END.

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